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Assessing patterns of oak regeneration and C storage in relation to restoration-focused management, historical land use, and potential trade-offs

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ABSTRACT

Restoration of composition, structure, and function in oak dominated ecosystems is the focus of management in temperate forests around the world. Land managers focused on oak ecosystem restoration are challenged by the legacy effects of complex land-use histories, urbanization, climate change, and potential stakeholder response to management. Trade-offs may exist between managing forests for climate mitigation (e.g., maximizing C storage or sequestration) and promoting shade-intolerant species historically associated with frequent or high-severity disturbances. This study assessed the potentially conflicting goals of sustained live biomass accrual and increased oak regeneration in the East Woods Natural Area at The Morton Arboretum in Lisle, IL, USA. We evaluated how biomass trends and oak regeneration were related to management regimes, land-use history, current stand structure and composition, and topoedaphic factors. Our results indicated no significant trade-off between sustained live biomass accrual and oak regeneration. Live biomass was increasing across the landscape (biomass increment averaged 18,186 kg ha^{-1} yr^{-1}) and was not strongly related to differences in management or land-use history. Oak regeneration was rare, especially beyond the seedling stage ($\sim$226 seedlings and 9 saplings ha^{-1}) and was also not strongly related to recent management. Our results indicate that even 20+ years of annual prescribed burning combined with understory thinning has failed to produce the open canopy conditions and high light availability that are necessary for successful oak recruitment. The absence of any trade-offs between biomass accrual and oak regeneration may, therefore, be largely related to the ineffectiveness of current management for promoting oak regeneration. More intensive management utilizing canopy manipulations could produce greater trade-offs, but is likely necessary to establish and release oak regeneration.

1. Introduction

The threat of climate change impacts on forest ecosystems is dramatically altering land management goals and practices (Millar et al., 2007). Land managers are adopting new management strategies designed to promote resiliency under future climate regimes with goals such as increasing carbon (C) sequestration and storage (mitigation) and diversifying species composition, increasing adaptive capacities, and maintaining successional pathways (adaptation) (D'Amato et al., 2011). These objectives have not displaced traditional objectives of wood production or ecosystem restoration, but instead are often expected to be accomplished in conjunction with them, despite potential conflicts. Effectively balancing multiple, often conflicting land management objectives can be difficult and is often viewed in a benefit-to-trade-off framework (Bradford and D'Amato, 2012). This study focused on evaluating patterns of C sequestration/storage in relation to management focused on increasing forest adaptation potential through promotion of oak regeneration and maintenance of oak canopy dominance.

Oaks are foundational species in forested ecosystems across the temperate zone, creating ecosystem structure, driving disturbance regimes, and supporting an array of plant and animal life (McShea and Healy, 2002; Rodewald and Abrams, 2002; Spetich, 2004). In such ecosystems, management focused on increasing climate resilience will often necessarily focus on maintaining oak dominance. Oaks are also important to mitigation-focused management in the region as they are large and long-lived and thus contribute disproportionately to stored carbon pools (Davies et al., 2011).

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However, oaks have declined in much of their former range, such as the Central Hardwoods region in the US, in part as a result of the removal of landscape fire regimes (Abrams, 1992; Bowles et al., 2005), although episodic drought from the 18th century may have contributed to establishing oak dominance in the region (Pederson et al., 2014).

Historical oak woodlands have transitioned to dense-canopied forests dominated by shade-tolerant species such as *Acer saccharum* (sugar maple) (often discussed as "mesophication"; Abrams, 1992; Nowacki and Abrams, 2008). These changes have been exacerbated by expanded herbivore populations (e.g., white-tailed deer; *Odocoileus virginianus*) and the invasion of exotic shrubs (e.g., *Rhamnus cathartica*; European buckthorn), which has greatly altered stand structure and nutrient cycling (Heneghan et al., 2006). In many areas, oak regeneration is exceedingly rare and pre-settlement legacy oaks are nearing their natural life-spans (Burns and Honkala, 1990). Without intervention, oaks may soon be lost from these systems or at least become a more minor component of the community (Fahey et al., 2012). Management focused on promoting oak regeneration will be necessary to maintain oak canopy dominance and associated ecosystem structure and services in the future, and is thus an important component of oak ecosystem restoration in general.

Successful oak regeneration requires moderate to high light levels, which can be limited by high densities of shade-tolerant trees or invasive shrubs (Lorimer, 1993; Lorimer et al., 1994). Such conditions can be hard to maintain in mesic forests, especially in natural areas or other protected lands where even-aged management treatments such as shelterwood harvests are not possible. Management to establish and promote oak regeneration in such areas generally involves understory control (Lorimer et al., 1994) and repeated prescribed fires (Bowles et al., 1994; Franklin et al., 2003). Repeated prescribed fire in combination with understory thinning might be sufficient to develop an oak regeneration layer if applied over a long enough time period, but there is a lack of information on the effect of repeated fire applied over long time periods (Arthur et al., 2012). Such treatments may be most likely to be successful on drier, less productive sites or sites with no encroachment of shade-tolerant species into the upper canopy (Johnson, 1984; Spetich et al., 2002; Iverson et al., 2008; Povak et al., 2008). In areas where shade tolerant species have become a component of the upper canopy and greatly reduced light levels to the understory, more intensive canopy removal treatments may be necessary (Iverson et al., 2008), which may decrease C storage in the short-term (McKinley et al., 2011).

Although management strategies for establishing and promoting oak regeneration are relatively well-understood – if not always easily implemented – the influence of land-use legacies can make it difficult to predict the specific impact of management on factors such as oak regeneration and C-sequestration/storage. Land-use changes can alter forest composition, structure, and processes, including biogeochemical cycling and hydrology (Fitzpatrick et al., 1999; Goodale and Aber, 2001), and these impacts can persist for hundreds to thousands of years (Dupouey et al., 2002; Foster et al., 2003). Land-use history could potentially affect both C storage and regeneration through effects on factors such as site productivity, understory structure, or regeneration microsites. Because of the pervasiveness of land-use impacts, defining the land-use history of a landscape is critical in providing insights for present-day management and restoration (Rhemtulla et al., 2009).

The overall objective of this research was to evaluate patterns of biomass accumulation and oak regeneration establishment under a variety of management regimes and in relation to land-use history. Specific objectives were to: (1) Quantify overall patterns of variation in C storage, canopy mortality, and oak regeneration, (2) Investigate the impact of specific restoration-focused management regimes and land-use histories on C storage, mortality, and oak regeneration (3) Assess specific drivers of variation in C storage, mortality, and oak regeneration, and (4) Examine potential trade-offs between C storage and oak regeneration.

2. Methods

2.1. Study area

This research was conducted in the ~240 ha East Woods Natural Area at The Morton Arboretum (hereafter 'East Woods') in DuPage County, Illinois, USA (41°49′0″N latitude and 88°3′0″W longitude). The climate is continental, with average temperatures ranging from −6 °C in January to 22 °C in July and mean annual precipitation of 800–1000 mm (Angel, 2011). The East Woods is located on the Valparaiso moraine complex. The soils are deep and moderately well to poorly drained Alfisols and Mollisols, formed in a thin layer of loess underlying glacial till (Kelsey, 2000). The East Woods site lies within the Prairie Peninsula (Transeau, 1935) and oak–hickory forest regions (Braun, 1950) and pre-settlement (early 1800s) forests in the region were highly oak dominated (Fahey et al., 2012) and characterized by a mixed-severity fire regime. The modern East Woods is densely forested with extensive dry-mesic upland forest dominated by white oak (*Quercus alba*), bur oak (*Quercus macrocarpa*), and red oak (*Quercus rubra*) and mesic forests on north-facing slopes dominated by sugar maple, basswood (*Tilia americana*), and other mesophytic species. The large oaks that dominate the canopy are mostly 140–175 years old and mean canopy age is estimated to be approximately 155 years (M. Bowles, unpublished data).

2.2. Management regimes

Across the East Woods, management units have been defined by The Morton Arboretum Natural Resources Management Program. These units are differentiated by their recent (~30 years) management regime, stand type (defined by topographical features), historical land-use, and boundaries formed by trails and roads. Restoration-focused management regimes include prescribed fire, understory thinning, and invasive shrub removal. Prescribed fire management has been implemented for >20 years and fire rotations range from annual burning to very infrequent (>10 year return interval; Table 1). Understory thinning (~80% removal of stems <20 cm diameter at breast height (1.37 m; DBH)) has been implemented to varying degrees in the units over the past ~10 years, with some units receiving nearly universal treatment and others entirely untreated (Table 1). Plots were classified into four, plot-level, management-type groups defined as: burned/thinned (BT), burned/unthinned (BU), unburned/thinned (UT), and unburned/unthinned (UU). Management-types were defined at the plot level because there was occasionally variable application of prescribed fire and other treatments within management units (i.e., treatment areas did not always conform to unit boundaries due to logistical and stakeholder-related concerns).

2.3. Land-use history

Land-use history for the East Woods was determined based on property deeds and decadal census data dating back to the original Euro-American settlement of the landscape in the early 1830s. For each property that overlapped the East Woods, a polygon was created in ArcGIS and based on information derived from the property deed and census data was assigned a date of acquisition and sale, coded into farmed/cleared, timber-lot, or other/unknown land-use, and assigned a date of transition into the holdings of

Table 1
Unit area, sample size, environment/management/land-use history characteristics, biomass patterns, and oak regeneration by management unit within East Woods Natural Area.

Unit	Unit area (ha)	Plots	Fire Freq. (yr^{-1})	% Thin	Mean open%	Farm% $	Live biomass ($kg\ ha^{-1}$)	ΔAGB* ($kg\ ha^{-1}$)	Mortality ΔAGB ($kg\ ha^{-1}$)	Recruit ΔAGB ($kg\ ha^{-1}$)	Survivor ΔAGB ($kg\ ha^{-1}$)	ANPP ($kg\ C\ ha^{-1}\ yr^{-1}$)	Oak seedlings		Oak saplings	
													Density (ha^{-1})	Relative density	Density (ha^{-1})	Relative density
Central woodland	14.2	18	0.08	83	5.8	0	303,334	24,561	2009	1707	24,597	2630	285.3	9.1	6.7	1.4
EW central	36.2	64	0.01	0	8.7	17	341,362	17,239	11,946	1164	27,830	2897	130.0	0.6	1.9	0.1
EW puffer	8.9	9	0.02	0	9.1	100	213,616	23,279	1476	3170	21,509	2445	35.6	0.1	8.9	0.6
EW unburned	9.7	18	0.01	0	9.0	94	198,300	8219	9106	1158	16,267	1733	460.0	2.5	0.0	0.0
Heritage	9.3	12	0.28	100	11.4	0	350,926	20,968	1920	1120	24,224	2514	100.0	6.1	3.3	2.3
Lacey bottoms	13.8	10	0.02	0	9.9	0	289,504	27,728	14,685	2592	38,096	4048	384.0	1.1	36.0	4.9
Ravine	16.2	18	0.02	67	10.2	0	255,798	23,582	8986	1407	30,776	3218	493.3	3.3	13.3	1.2
South forty	19.4	26	0.90	0	10.1	88	227,078	20,965	2948	2510	21,224	2363	170.8	9.2	0.0	0.0
Triangle	12.6	7	0.06	14	10.2	0	329,327	12,070	18,384	2064	28,379	3013	502.9	2.2	0.0	0.0
Woodland	16.2	32	0.01	13	9.2	13	262,038	16,096	1156	1665	15,767	1734	175.0	9.5	31.3	4.5
Total/Average	**156.5**	**220**	**0.14**	**20**	**9.2**	**30**	**277,746**	**18,186**	**7054**	**1601**	**23,595**	**2512**	**225.9**	**1.6**	**8.9**	**0.3**

@Transformation of slope and aspect that estimates levels of solar radiation incident on a slope (McCune and Keon, 2002).
% Based on hemispherical canopy photographs analyzed with Gap Light Analyzer v2 (Frazer et al., 1999).
* Integrated Moisture Index – based on hillslope layers from Digital Elevation Model (Iverson et al., 1997).
$ Based on historical land use records collected by The Morton Arboretum Natural Areas management program.

The Morton Arboretum. Based on this information, management units were classified into categories describing the general pattern over time ("temporal land-use category"; e.g., land used as timberland that then transitioned to farmland would be classified as "Timber-Farm") with each pattern ending with incorporation into the East Woods. Temporal land-use categories included: Timber-Farm, Farm-Timber, Farm-only, and Timber-only.

2.4. Data collection

Sampling was conducted in 2006 and 2011 on a network of circular 250 m^2 permanent plots randomly located at intersections on a grid network that spans the East Woods – total sample size was 220 plots. Visual estimates were made for ground cover (bare soil, litter, coarse woody debris, water, tree boles, rock, and trails and roads), percent herb cover, percent shrub cover, and average shrub height for the full plot. All trees ($\geqslant$10 cm DBH) within the full plot (8.9 m radius) were inventoried for species and DBH, saplings ($\geqslant$1.37 m in height, <10 cm DBH) were tallied by size class (0–4.9 cm DBH and 5–9.9 cm DBH), and seedlings (<1.37 m in height) were tallied in a 30 m^2 sub-plot (3.1 m radius). In 2011, for all oak seedlings within the full plot (8.9 m radius) we recorded species, height, basal diameter, and current year growth (determined by length from apical meristem to most recent annual internode).

To assess the understory light environment, hemispherical images were collected in four locations in each plot at 1.5 m above ground level with an 180° fish-eye lens on a tripod-mounted Nikon Coolpix 800 digital camera under uniformly cloudy sky conditions. Each image was processed using Gap Light Analyzer (GLA) software (Frazer et al., 1999) to calculate percent canopy openness. For each plot, Integrated Moisture Index (IMI; (Iverson et al., 1997) was calculated as a function of slope, aspect, elevation, hillshade, flow accumulation, and curvature based on USGS digital elevation model in ArcGIS. In addition, Heatload Index was calculated for each plot location based on slope and a transformation of aspect based on the methods of McCune and Keon (2002).

2.5. Data analysis

Stem density was calculated for each plot and management unit for all three layers (seedling, sapling, overstory) and both sampling dates. For overstory trees ($\geqslant$10 cm dbh), we also calculated plot and management-unit-level basal area and live biomass. Live biomass was estimated using generalized diameter to biomass regression equations from Jenkins et al. (2003). Data from the two inventories were compared in order to quantify changes in stem density, basal area increment (BAI), aboveground live biomass increment (BMI), mortality (rate and biomass lost), recruitment (rate and biomass added), and ANPP.

Change in aboveground biomass (ΔPLOTAGB) was calculated by monitoring the increments for each individual tree using the following formula (Clark et al., 2001):

$$\Delta \mathrm{PLOTAGB} = \sum_{i=1}^{n}(\mathrm{AGBT2}i - \mathrm{AGBT1}i) + \sum_{j=1}^{k}(\mathrm{IngAGB}j - \mathrm{AGBMIN}j) \quad (1)$$

where $\mathrm{AGBT2}_i$ is the plot-level aboveground biomass of tree *i* at the end of the measurement interval, $\mathrm{AGBT1}_i$ is the aboveground biomass of tree *i* at the beginning of the measurement interval, IngAGB_j is the aboveground biomass of ingrowth tree *j* and AGBMIN is the biomass of the ingrowth tree *j* when its diameter was at the minimum (10 cm). ANPP ($kg\ C\ ha^{-1}\ yr^{-1}$) was estimated by dividing ΔPLOTAGB for all surviving and ingrown trees by the difference between the end (*T*2) and beginning (*T*1) of the measurement interval:

$$\mathrm{ANPP} = 0.5 \times \frac{\sum_{i=1}^{n}(\mathrm{AGBSurT2}i - \mathrm{AGBSurT1}i) + \sum_{j=1}^{k}(\mathrm{IngAGB}j - \mathrm{AGBMIN}j)}{T2 - T1} \quad (2)$$

The coefficient 0.5 in Eq. (2) was applied to convert the dry mass to carbon produced, assuming 50% of plant tissues were carbon (Penman et al., 2003).

To assess compositional patterns and trajectories of compositional change between the two measurement periods, we conducted nonmetric multidimensional scaling (NMS) ordination on matrix of species basal area by management unit that included the 2006 and 2011 samples as separate data points. NMS was performed using PC-ORD v.5.31 (McCune and Mefford, 2006) with the "slow-and-thorough" auto-pilot setting, using 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution. Unit-level data points for the two time periods were graphed together in ordination space to illustrate change in species composition between time periods relative to overall among unit compositional differences.

To assess the effect of management and land-use history on ANPP, mortality and oak regeneration (Objective 2), ANPP and canopy mortality rates and characteristics of the oak regeneration population (density, relative density, mean growth rate) were compared among management units, management-type groups, and land-use history groups with ANOVA using PROC GLM in SAS v. 9.2 (SAS-Institute, 2005). Individual group comparisons were made using the Tukey–Kramer adjustment for multiple comparisons.

To evaluate drivers of ANPP and oak regeneration (Objective 3), data from the 2011 survey and the comparison of 2006 vs. 2011 were related to management and site characteristics. Multiple linear regression in an information-theoretic framework (Burnham and Anderson, 2002) was used to test a set of *a priori* models regarding the effect of a suite of management and site characteristics on ANPP and oak regeneration (using PROC MIXED in SAS). Potential drivers of ANPP included overstory stem density, fire frequency, overstory basal area, overstory species composition (NMS ordination axes), overstory mortality rate, mean diameter, stem size diversity (Shannon diversity index of diameter class counts), IMI, canopy openness, and Heatload Index. Potential drivers of oak regeneration included herbaceous cover, shrub cover, shrub height, overstory stem density, fire frequency, overstory basal area, overstory species composition (NMS ordination axes), IMI, canopy openness, and Heatload Index. For both factors, a set of plausible models was evaluated using the corrected Akaike Information Criterion (AIC_c). AIC_c is derived from the maximum log-likelihood estimate and number of parameters in a given model, penalizing models for lack of fit and multiple parameters (lower values indicate better models). Models were ranked by the difference between the AIC_c value for the model and the lowest value in the full model set (ΔAIC_c), which included the null model. This method allows for comparison of the strength of evidence among the models, with increasing ΔAIC_c values indicating decreasing probability of the fitted model being the best model in the set. Models with ΔAIC_c <2 are considered to have substantial support and models above this threshold are generally not interpreted (Burnham and Anderson, 2002). To approximate the probability of a model being the best in a given set, ΔAIC_c values were used to calculate Akaike weights using the following formula:

$$w_i = \frac{\exp(-\Delta AIC_c/2)}{\sum_{r=1}^{R} \exp(-\Delta AAIC_c/2)} \tag{3}$$

where w_i is the Akaike weight for model i and R is the number of models in the set.

To evaluate trade-offs between ANPP and oak regeneration (Objective 4) linear regression was used to assess the relationship between ANPP and characteristics of the oak regeneration pool (density, relative density, mean growth rate, total basal area). We assessed both linear and non-linear model fits using Sigmaplot v. 13 (SYSTAT, 2014).

3. Results

3.1. Biomass trends

Overall, there was a positive BMI for the East Woods as a whole (18,186 kg/ha; Table 1) with BMI of survivors (23,595 kg/ha) and recruits (1601 kg/ha) outpacing losses to mortality (7054 kg/ha). Live biomass also increased within each individual management unit, but there was significant variation among units in BMI (maximum of 27,728 kg/ha in Lacey, minimum of 8219 kg/ha in EW Unburned; Table 1). The Lacey and Triangle units had especially high mortality, but this mortality was balanced by especially high ANPP in these locations (Table 1). ANPP varied strongly among management units based on ANOVA ($F_{9,188} = 3.51$, $p < 0.001$), as did canopy mortality rate ($F_{9,205} = 3.23$, $p = 0.001$). Neither factor varied among management-type groups: ANPP ($F_{3,194} = 0.87$, $p = 0.46$), canopy mortality rate ($F_{3,211} = 0.19$, $p = 0.90$). ANPP did not differ among historical land use categories ($F_{3,193} = 0.95$, $p = 0.42$; Fig. 1), while canopy mortality differed marginally ($F_{3,210} = 2.32$, $p = 0.08$).

All species had positive BMI except for elm (*Ulmus* spp.; probably related to continued losses from Dutch Elm Disease; Table 2). Ashes (*Fraxinus* spp.) had high mortality due to initial losses to Emerald Ash Borer (*Agrilus planipennis*), but survivor trees were highly productive resulting in positive BMI. Sugar maple had the highest BMI and also exhibited a large increase in stem density. White oak had very high ANPP, but this was balanced by high levels of mortality. Among the less dominant species, silver maple (*Acer saccharinum*) had an especially high BMI, while ironwood (*Ostrya virginiana*) had a large increase in stem density.

The ordination of 2011 composition had a three-dimensional solution that explained 97.6% of the variation in the original data matrix and was highly significant based on Monte Carlo tests ($p = 0.02$, Stress = 0.35; Fig. 2a). Compositional differences among management units were related to a number of factors, both edaphic and historical (Fig. 2a). For example, Ravine Woods (RW) had a component of trees planted into forestry plots in the early years of Morton Arboretum ownership including: red pine (*Pinus resinosa*), Norway spruce (*Picea abies*), Kentucky yellowwood (*Cladrastis kentuckea*) and tulip poplar (*Liriodendron tulipifera*). Central Woods had a combination of ornamental species escaped from cultivation in nearby horticultural collections such as eastern redbud (*Cercis canadensis*) and Ohio buckeye (*Aesculus glabra*) in addition to the native forest assemblage of shagbark hickory (*Carya ovata*), white oak, red oak, and black cherry (*Prunus serotina*). East Woods Unburned and East Woods Central both occur on northern slopes, have high IMI, and have little history of fire management; all of which have promoted high levels of shade tolerant, mesic species such as sugar maple and basswood. In general, there was very little change in species composition within management units based on

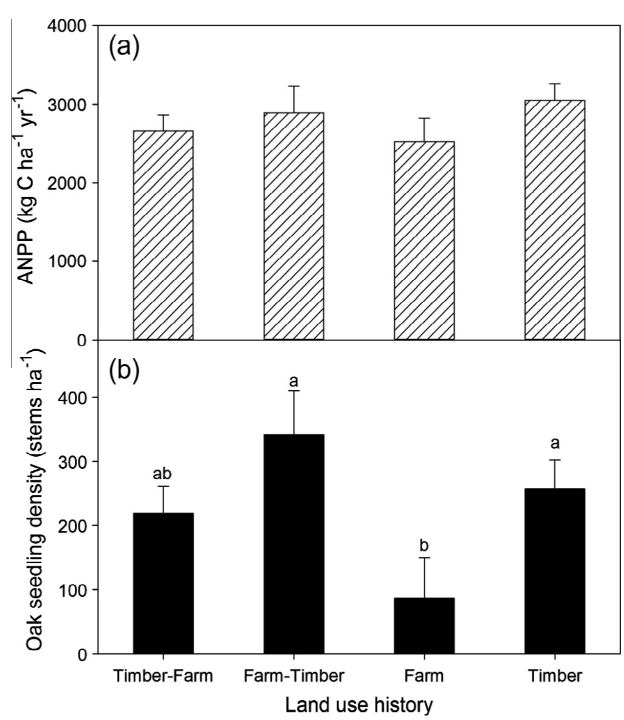

Fig. 1. Aboveground net primary productivity (ANPP) (a) and oak seedling density (b) by temporal land-use history categories. ANOVA for ANPP ($F_{3,211} = 0.95$, $p = 0.42$) and for oak seedling density ($F_{3,212} = 2.97$, $p = 0.03$). Letters indicate results of individual comparisons in ANOVA model – common letters indicate no significant difference between units following Tukey–Kramer adjustment for multiple comparisons.

Table 2
Estimates of stem density, aboveground biomass, change in biomass for pools between 2006 and 2011, and annual aboveground production (ANPP) by species in the East Woods Natural Area.

Species	Density 2006 (stems ha^{-1})	Density 2011 (stems ha^{-1})	Live biomass 2011 (kg ha^{-1})	ΔAGB* (kg ha^{-1})	Mortality ΔAGB (kg ha^{-1})	Recruit ΔAGB (kg ha^{-1})	Survivor ΔAGB (kg ha^{-1})	ANPP# (kg C ha^{-1} yr^{-1})
Quercus alba	38.7	38.7	102663.5	4559.0	2789.5	0.0	7348.5	734.8
Quercus rubra	24.4	25.6	47797.6	3454.2	1351.7	64.2	4731.9	479.6
Acer saccharum	92.0	105.3	42532.9	5177.9	138.3	636.3	4663.6	530.0
Quercus macrocarpa	10.2	10.4	32999.1	2079.1	0.0	7.1	2072.0	207.9
Fraxinus spp.	31.6	33.8	17939.8	1298.2	940.2	50.4	2162.6	221.3
Tilia americana	42.0	48.9	11163.0	1364.6	326.5	243.3	1426.8	167.0
Prunus serotina	30.7	32.7	4280.9	132.1	324.1	77.7	378.4	45.6
Ulmus spp.	28.5	35.6	4134.2	−161.9	803.8	228.4	390.6	61.9
Acer saccharinum	3.6	4.7	3640.5	839.8	0.0	64.8	775.0	84.0
Juglans nigra	2.0	2.2	3136.1	332.5	0.0	8.4	324.1	33.3
Ostrya virginiana	20.7	25.8	1395.0	271.6	71.6	176.4	166.8	34.3

* Estimated change in aboveground biomass.
# Estimated annual aboveground net primary productivity.

the NMS ordination analysis (Fig. 2b). The ordination of combined 2006 and 2011 composition had a three-dimensional solution that explained 98.3% of the variation in the original data matrix and was highly significant based on Monte Carlo tests ($p = 0.008$, Stress = 1.84; Fig. 2b).

In the multiple regression modeling of ANPP, the most highly supported models (models 1–4 with $\Delta AIC_c < 2$; Table 3) included combinations of the following predictors: initial basal area, canopy openness, species composition (NMS ordination axis 3), and IMI. These four models were much stronger than null model ($\Delta AIC_c = 297.7$) and accounted for 66% of the weighting in the model set (Table 3). The "best" model among these had high weighting ($w_i = 0.30$) and moderate power in predicting ANPP at the plot-level ($R^2 = 0.41$). Based on this analysis, ANPP at the plot-level was higher with greater initial basal area, greater canopy openness, silver maple and basswood components, and wetter sites.

3.2. Oak regeneration

Oak seedling density was generally low with an average of only 226 stems/ha across all management units and a maximum of 503 stems/ha in the Triangle unit (Table 1). Relative density (percent of total seedling stems) was also generally very low with an average of 1.6% overall and a maximum of 9.5% in the Woodland unit. There was a general inverse relationship between oak seedling density and relative density, as units with high oak seedling density all had low (<4%) relative density (Table 1). Oak seedling density was slightly higher with lower fire frequency (Fig. 3) while relative density was higher with high fire frequency (but in both cases ANOVAs comparing fire frequency groups were non-significant: $F_{3,213} = 1.26$, $p = 0.29$ and $F_{3,213} = 1.34$, $p = 0.26$ respectively).

There were significant differences among management units in oak seedling density ($F_{9,206} = 3.74$, $p < 0.001$) and oak seedling relative density ($F_{9,206} = 3.64$, $p < 0.001$). Oak seedling density was highest in the Central Woodland, EW Unburned, Lacey Bottoms, Ravine, and Triangle management units (Table 1). However, the ANOVAs comparing oak regeneration among management type groups were not significant: oak seedling density ($F_{3,213} = 0.32$, $p = 0.81$); oak seedling relative density ($F_{3,213} = 1.03$, $p = 0.38$). ANOVAs testing for differences among land-use history groups found a significant difference for oak seedling density ($F_{3,212} = 2.97$, $p = 0.03$; Fig. 3), but not oak seedling relative density ($F_{3,212} = 1.82$, $p = 0.14$).

In the multiple regression modeling of the drivers of oak seedling density, the most highly supported models (models 1 & 2 with $\Delta AIC_c < 2$; Table 3) included combinations of the following predictors: initial basal area, shrub height, species composition (NMS ordination axis 1), and IMI. These two models were much stronger than the null model and accounted for 80% of the weighting in the model set (Table 3). The "best" model among these had high weighting ($w = 0.49$) relative to the model set as a whole, but had very low power in predicting oak seedling density ($R^2 = 0.05$).

3.3. Trade-offs

Plot-level linear regressions indicated no significant relationships between ANPP and characteristics of the oak regeneration pool: oak seedling density ($r = 0.02$), oak seedling relative density ($r = -0.14$), oak seedling growth ($r = 0.07$), oak seedling height ($r = 0.02$), and oak sapling relative density ($r = -0.04$). Non-linear models were not significantly more predictive than linear models for any of the comparisons. Management-unit-level regression analysis indicated that oak seedling relative density was somewhat negatively related to ANPP ($r = -0.46$; Fig. 4), but this relationship was non-significant ($p = 0.18$) probably due in part to the small sample size and low power of the test.

4. Discussion

This study found biomass aggradation in this 150+ year old stand and little oak regeneration even after long-term, repeated annual prescribed fire management. As such, there were no strong trade-off between the two potentially conflicting management objectives of maintaining positive biomass increment and promoting oak regeneration. Previous studies have shown some degree of trade-offs between C storage and features that might increase adaptive capacity such as structural and compositional complexity (D'Amato et al., 2011; Bradford and D'Amato, 2012; Burton et al., 2013; Seidl and Lexer, 2013), but did not specifically address regeneration as an adaptive factor. The lack of trade-offs in this study may be somewhat related to the low-intensity of management and lack of disturbance-caused mortality of overstory trees in the system. In most research that has illustrated trade-offs, the focus has been on forests managed for wood production or a combination of wood production and other benefits (Bradford and D'Amato, 2012). Management in this protected ecosystem has consisted of low-intensity treatments such as prescribed fire and understory thinning. These treatments appear to have been insufficient for establishing oak regeneration and creating open canopy conditions. This is the case even where these treatments have been applied in combination over long time periods (20+ years). This

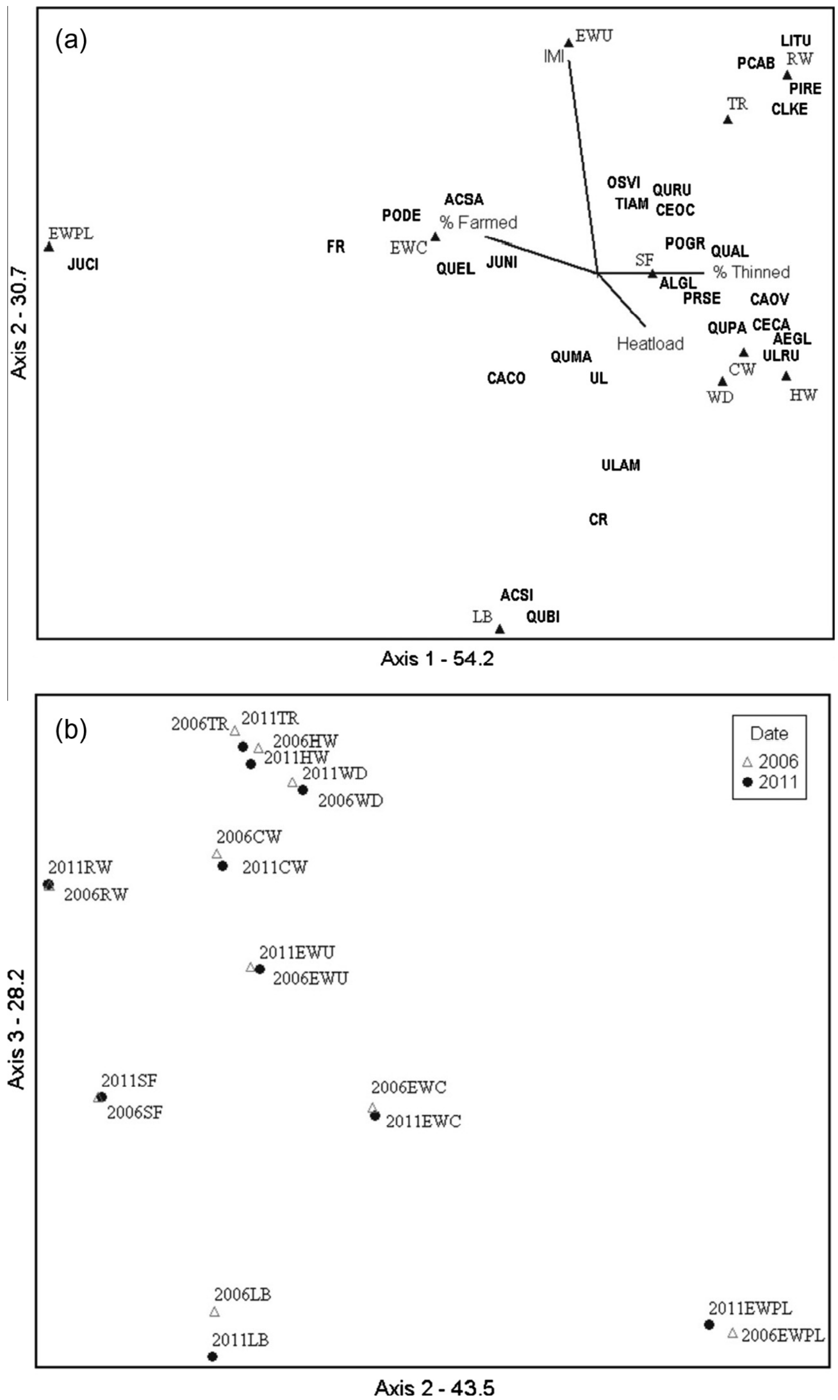

Fig. 2. NMS ordination of (a) management-unit-level species composition in 2011 with overlay vectors indicating association of environmental variables with solution and (b) combined 2006 and 2011 data. Numbers next to axis names indicate percent of variance in original matrix explained by the axes. Full results can be found in text. Unit acronyms: CW – Central Woodland, EWC – East Woods Central, EWPL –East Woods Puffer, EWU – East Woods Unburned, HW – Heritage, LB – Lacey Bottoms, RW – Ravine, SF – South Forty, TR – Triangle, WD – Woodland. Species acronyms: ACSA – *Acer saccharum*, ACSI – *A. saccharinum*, AEGL – *Aesculus glabra,* ALGL – *Alnus glutinosa,* CACO – *Carya cordiformis,* CAOV – *C. ovata,* CECA – *Cercis canadensis,* CEOC – *Celtis occidentalis,* CLKE – *Cladrastis kentuckea,* CR – *Crataegus* spp., FR – *Fraxinus* spp., JUCI – *Juglans cinerea,* JUNI – *J. nigra*, LITU – *Liriodendron tulipifera,* OSVI – *Ostrya virginiana*, PCAB – *Picea abies*, PIRE – *Pinus resinosa*, PODE – *Populus deltoides*, POGR – *P. grandidentata*, PRSE – *Prunus serotina*, QUAL – *Quercus alba* QUBI – *Q. bicolor,* QUEL – *Q. ellipsoidales,* QUMA – *Q. macrocarpa,* QUPA – *Q. palustris,* QURU – *Q. rubra,* TIAM – *Tilia americana*, UL – *Ulmus* spp., ULAM – *U. americana,* ULRU – *U. rubra.*

result suggests that programs that rely on long-term application of repeated, low-intensity prescribed surface fire may not always be sufficient to promote oak regeneration (Arthur et al., 2012). Canopy mortality was very low across the landscape and canopy openness and light transmittance were also ubiquitously low. Overstory management treatments or disturbances that, in conjunction with artificial regeneration, could create the conditions necessary to promote oak regeneration may be more likely to lead to trade-offs with C-storage and ANPP. Also, although there were no trade-offs between ANPP and oak regeneration, there may be trade-offs with other features of the forest that could promote ecosystem resiliency, and that are important aspects of a general oak ecosystem

Table 3
List of most highly supported models from multiple regression analysis of plot-level aboveground productivity (ANPP) and plot-level oak seedling density. Models with ΔAIC_c <2 are considered to be highly supported (Burnham and Anderson, 2002).

Factor	Rank	Predictors[a]	k[#]	AIC_c[#]	ΔAIC_c	w_i[#]
ANPP						
	1	CanOpen, BA	4	2666.2	0.00	0.30
	2	NMS3, CanOpen, BA	5	2667.8	1.58	0.14
	3	NMS3, CanOpen, BA	5	2667.8	1.99	0.11
	4	BA, IMI	4	2668.2	2.08	0.11
	5	MeanDBH, CanOpen, BA	5	2668.3	2.44	0.09
Oak regeneration						
	1	NMS1, ShrubHt, IMI	5	2917.5	0.00	0.49
	2	BA, ShrubHt, IMI	5	2918.4	0.94	0.31
	3	NMS1, CanOpen, ShrubHt	5	2920.2	2.76	0.12
	4	NMS1, HerbCov, CanOpen, ShrubHt	6	2922.0	4.55	0.05
	5	NMS1, HerbCov, CanOpen, BA, ShrubHt	7	2924.0	6.57	0.02

[#] k – number of model parameters, AIC_c – Corrected Akaike Information Criterion, w – Akaike weights – see text for details (Burnham and Anderson, 2002).
[a] CanOpen – Canopy openness from hemispherical photographs, NMS1/NMS3 – primary axes from ordination of species composition by plot, BA – basal area, IMI (Integrated Moisture Index), MeanDBH – mean diameter at 1.37 m height, DBHDiv – Shannon Diversity Index of diameter classes (5 cm classes), MortRate – canopy tree mortality rate, FireFreq – frequency of fire for period with management records (20 years), ShrubHt – mean height of shrub layer, ShrubCov – plot-level shrub layer cover (>1 m height), HerbCov – plot-level herbaceous layer cover (<1 m height), OverDen – density of overstory stems (>10 cm dbh), HeatLoad – heat load index (McCune and Keon, 2002).

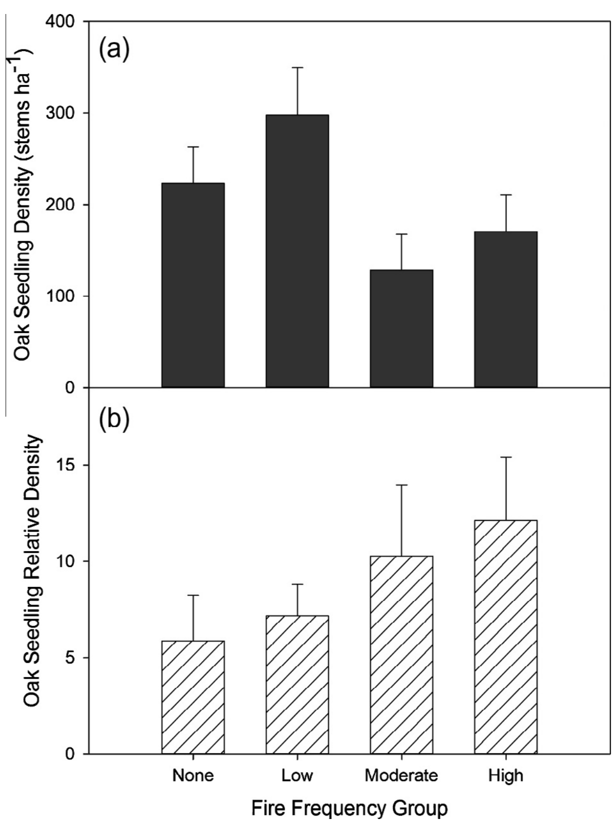

Fig. 3. Oak seedling density (a) and relative density (b) at the plot-level by fire frequency group – low = <0.1 fires yr^{-1}, moderate $\geqslant 0.1 \leqslant 0.3$, high >0.3. ANOVAs comparing fire frequency groups were non-significant for seedling density ($F_{3,213}$ = 1.26, p = 0.29) and relative density ($F_{3,213}$ = 1.34, p = 0.26).

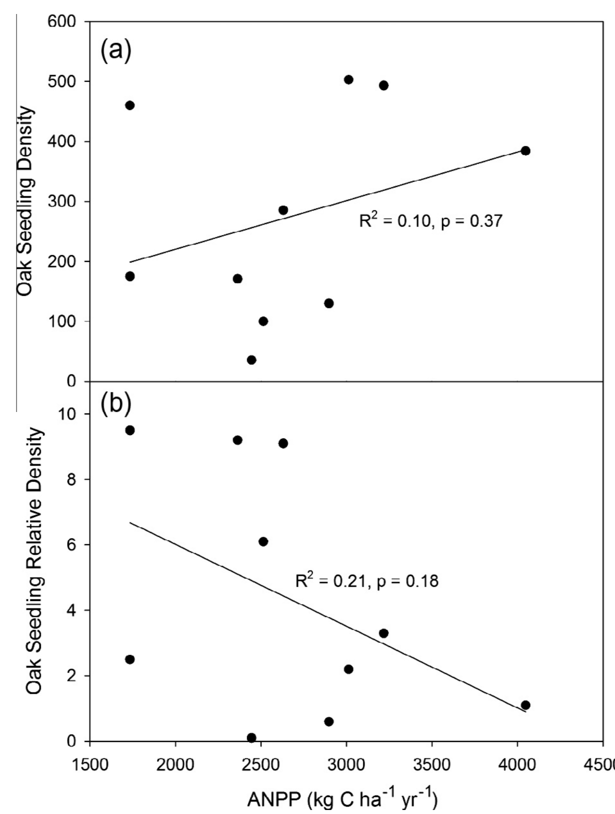

Fig. 4. Scatterplot of management unit-level oak seedling density (a) and relative density (b) vs. aboveground net primary productivity (ANPP).

restoration program, such as groundlayer diversity, wildlife habitat, or canopy structural complexity (D'Amato et al., 2011; Burton et al., 2013).

4.1. Trends in biomass and mortality

Our data indicate that the East Woods is continuing to accrue biomass and sequester C despite being relatively old (~155 years old; M. Bowles, unpublished data) compared to other forests in the region. Estimated ANPP averaged 2512 kg C ha^{-1} yr^{-1} across all management units. The forests of the East Woods may not have reached their age-related decline in production (Gower et al., 1996), but these levels of ANPP are somewhat low for oak forests in the Central Hardwood region. For example, Chiang et al. (2008) illustrated ANPP in unthinned sites ranging from 3400 to 5600 kg C ha^{-2} yr^{-1} and Newman et al. (2006) 2570 to 5780 kg C ha^{-2} yr^{-1}. However, these examples come from younger, managed forests rather than natural areas. Belowground NPP and net ecosystem production (NEP) were not measured, but the current low amount of coarse woody debris and snags (CWD volume = 34.2 m^3 ha^{-1} and snag basal area = 1.6 m^2 ha^{-1}) suggest against especially high ecosystem respiration. In the coming decades, as the oak trees that are the largest contributors to the BMI and ANPP (Table 2) approach the end of their lifespans, we expect a drop in gross primary production (GPP) and increases in CWD inputs and associated respiration, which could reduce NEP.

Differences in management regimes did not appear to have a strong effect on biomass trends or mortality. Presently, differences in ANPP among management units appear to be related primarily to species composition and structural differences that existed prior to recent management interventions and are likely associated with pre-settlement vegetation and historical land-use. There was also some evidence for topoedaphic effects on ANPP, but neither IMI nor Heatload were very strong predictors of among-plot differences in ANPP (Table 3). The lack of a management effect is probably partly related to the relatively low intensity of treatments that have been applied. For example, two decades of annual, low-intensity prescribed fires in the South Forty unit have not yet affected live biomass or canopy mortality rates. The canopy mortality rate in this unit was among the lowest in the study, suggesting little attrition from repeated low-intensity prescribed fire even over relatively long time periods, which may not match common conceptions held by many land managers. Management in oak-dominated natural areas may increase in intensity in the future as managers shift to a focus on promoting oak regeneration (Fahey et al., 2012), with activities such as canopy thinning to promote artificial regeneration leading to higher mortality rates and more impact on C dynamics.

Age-related decline and the spread of exotic pests will also likely have an impact on biomass and canopy mortality. White oak accounted for the greatest proportion of overall ANPP, but also had especially high levels of mortality, which may represent the beginning of age-related decline in these older canopy trees. Likewise, the pending loss of ashes to emerald ash borer will likely affect biomass and species composition (Desantis et al., 2012), but this impact is not expected to be very significant in the long-term because ash comprises a relatively small proportion of the forest (Table 2). Other pests and disease such as Asian long-horned beetle (*Anoplophora glabripennis*), oak wilt (*Ceratocystis fagacearum*), or gypsy moth (*Lymantria dispar dispar*), would have a much greater impact due to the dominance of their primary host genera (maples and oaks, respectively). These potential future sources of mortality could lead to depressed C sequestration and biomass accumulation rates, but some studies have illustrated high resiliency of C sequestration to successional transition or dispersed mortality (Gough et al., 2008).

4.2. Oak regeneration

There was little oak regeneration in this landscape, with seedlings rare (226 stems ha^{-1}) and saplings almost totally absent (9 stems ha^{-1}), despite management efforts designed, in part, to promote oak regeneration establishment in preparation for release through canopy manipulations. Oaks also represented a very small component of these layers overall (relative density for seedlings 1.6% and for saplings 0.3%) and there was little ingrowth of oaks into the overstory tree layer (only 4.6% of total recruit biomass), especially in relation to other tree species such as sugar maple (Table 2). These findings align with findings elsewhere of a bottleneck in oak regeneration and understory dominance by shade tolerant species in oak ecosystems (Lorimer, 1981; Pubanz et al., 1989; Nowacki et al., 1990). However, our seedling numbers are low in relation to many published reports. For example, Götmark (2007) recorded approximately 9000 oak seedlings per hectare the year following a mast year. Iverson et al. (2008) found roughly 15,000 oak and hickory seedlings (<10–50 cm in height) per hectare on sites with an intermediate IMI class that had been burned, and roughly 18,000 seedlings (<10–50 cm in height) per hectare on sites that had been thinned. Iverson et al. (2008) also found oak and hickory saplings (140 cm in height to 2.9 cm DBH) to be nearly absent pre-treatment and then to increase to an average of 80 and 120 stems ha^{-1} on treated intermediate and dry plots, respectively. This response was certainly aided by the significant oak seedling layer, a feature which is absent from the East Woods, which limits management options in the system and will likely necessitate artificial regeneration prior to mechanical canopy manipulations.

Management efforts to date appear to have affected stand structure to some extent, but have not strongly influenced oak regeneration. One major reason for this pattern is that management has not led to canopy mortality and associated higher light transmittance. Light levels were consistently low throughout the East Woods (unit max of 11% canopy openness; plot max of 27%; only two plots had higher than 15%). Arthur et al. (2012) suggest that "When fire is the only feasible management tool available, repeated fire may provide a suitable means for improving oak regeneration", but also that there is high level of uncertainty about the effectiveness of such a program. In this system, conditions for oak regeneration were not positively impacted even after 20 years of annual prescribed fire, suggesting against the effectiveness of repeated prescribed surface fire for stimulating oak regeneration, at least in these dry-mesic forests.

There was some variation in oak regeneration among management units, but not management types, suggesting more of a site and species composition effect than a management effect. Low IMI and high overstory oak dominance both weakly predicted the presence of oak regeneration, which likely reflects the greater seedling pool in areas with a seed source or conditions less amenable to sugar maple dominance. Shrub layer height was a significant predictor of oak seedling density, which may indicate an effect of management activities that was not reflected in the analysis of management-type groups. Other studies have shown that high shrub layer competition can negatively affect oak regeneration (Lorimer et al., 1994). A related reason that management type may have been non-significant is that areas with high initial levels of invasive shrubs were most likely to be targeted for management, which would result in more similar growing conditions among units rather than differentiation.

Another potential reason that management was not strongly related to oak regeneration is that fire management can also have negative effects on oak regeneration – through repeated direct top-kill – even as conditions become more amenable for these seedlings (Brose et al., 2014). This pattern is apparent in the lack of a relationship between fire frequency and oak seedling density and the corresponding slight positive relationship with relative density (Fig. 3). A specific example of this pattern can be seen in the annually burned South Forty unit, which had low oak seedling density – but high oak seedling relative density related to very low overall seedling densities (Table 1). This unit also had the lowest seedling height – which likely relates to the repeated top-kill and turnover associated with annual burning. The South Forty unit also had low shrub cover (14% vs. mean of 25%) and height (0.55 m vs. mean of 0.91), indicating the influence of fire in regulating shrub cover.

4.3. Land-use effects

The various parcels that make up the modern-day East Woods underwent a range of land-use histories over a span of over 200 years and historical timber harvesting, agriculture, and grazing have all contributed to shaping the landscape. However, the land-use history classes used in this study did not explain variation in ANPP or oak regeneration, suggesting against a strong legacy effect of historical land-use in this system. The lack of a relationship could be due to the very general classes used in the analysis, which were necessitated by the convoluted and, often times, anecdotal evidence that exists for land-use history at a fine scale. Also, the land-use patterns in the East Woods are relatively similar, as grazing and harvesting likely affected all areas that were not cleared, and the variables measured here may not be the most likely to respond to past land-use differences (relative to soil factors or groundlayer communities). There is also likely a strong legacy effect of pre-urban vegetation – which has been shown to impact the composition of modern vegetation communities, even in highly urbanized landscapes (McBride and Jacobs, 1986; Fahey et al., 2012). These legacy effects may swamp some of the specific historical land-use effects and, in addition to variability in site conditions (slope, aspect, IMI, etc.), are likely behind the compositional and initial basal area differences that were the strongest predictors of variation in ANPP and oak regeneration. Finally, recent management practices may have overridden the effects of historical land-use to some extent.

4.4. Management implications

More intensive treatments focused on canopy structure, such as mechanical canopy thinning targeting shade-tolerant species, are often necessary to promote successful oak canopy recruitment (Iverson et al., 2008; Dey et al., 2010). Such treatments can be used to mimic the effects of mixed-severity fire regimes and to create conditions more similar to those that would exist without 100+ years of fire suppression (Nowacki and Abrams, 2008). Our results suggest that such treatments are likely to be necessary in the establishment phase in dry-mesic forests, and possibly in conjunction with artificial regeneration. Canopy thinning could have short-term negative impact on ANPP and C-storage, but may have a positive effect in the mid- to long-term (McKinley et al., 2011). However, land managers must balance the ecological needs of oak regeneration and biomass production with the aesthetic and recreational needs of the public. This is especially true in urban areas or on protected lands, such as the study area detailed here. Understanding the conditions that promote oak regeneration in the landscape can help prioritize areas for management and decrease both total effort and the potential for conflicts with other priorities. For example, limiting management interventions in more mesic stands within the landscape could help buffer the overall effects of intensive management elsewhere – such as drier, south-facing stands that are more likely to support oak regeneration. Intensifying management efforts in such areas through higher severity prescribed fires, mechanical canopy manipulations, and artificial regeneration methods may promote oak regeneration establishment and recruitment while limiting impacts on landscape-level C storage or recreational value.

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