

The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net primary production of overstory trees in an oak-hickory ecosystem in southern Ohio

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Abstract

More than 70 years of fire suppression has influenced forest dynamics and led to the accumulation of fuels in many forests of the United States. To address these changes, forest managers increasingly seek to restore historical ecosystem structure and function through the reintroduction of fire and disturbance processes that mimic fire such as silvicultural thinning. In oak forests of eastern North America, prescribed fire and thinning are important tools used to facilitate oak (*Quercus* spp.) regeneration and recruitment. The global scientific community is increasingly raising concerns about the accumulation of atmospheric CO₂, and its potential to impact global climate; therefore, activities such as prescribed fire and thinning that can influence the carbon balance of terrestrial ecosystems should be evaluated. We used field measurements and modeling with the PnET-II carbon balance model in oak forests of southern Ohio, USA, to (1) assess the efficacy of prescribed fire and silvicultural thinning in facilitating oak recruitment and regeneration, and (2) quantify the impacts of these treatments on aboveground carbon stocks and net primary production. Silvicultural thinning increased recruitment of maples, but oak recruitment was minimal. Prescribed burning caused an increase in the mortality rate of oaks' major competitor (*Acer rubrum* L.) in the overstory (stems ≥ 10 cm DBH), but oak mortality also increased following the burn treatments. Our measurements of stem growth suggest that the timing of the prescribed fires coincided with the initiation of growth in oaks, which may have created vulnerability in these species that are generally considered fire-resistant. The pre-treatment aboveground biomass of overstory trees was approximately 233 Mg/ha (Mg = 1×10^6 g). Prescribed burning had significant impacts on the mortality of stems; however, it had no significant effects on the aboveground net primary production (ANPP). Thinning removed approximately 30% of the aboveground biomass and resulted in significant but transient (1 year) reduction of ANPP (386 and 560 g C m⁻² year⁻¹ for thinned and non-thinned stands, respectively). In sum, thinning created recruitment opportunities in our study area, but these opportunities were captured by maples, and oak recruitment was minimal. Prescribed fire caused mortality in oaks and maples, and the oak mortality may have been related to the coincidence of the burn treatment and the initiation of oak stem growth. Finally, our data suggest that there is a transient impact of thinning on ANPP, but that there is no long-term effect of thinning and/or burning treatments on the aboveground carbon uptake in oak forests.

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1. Introduction

Many forests in the United States have experienced periodic fires for the last several thousand years (Pyne, 1982; Delcourt et al., 1998; Shumway et al., 2001; Fule et al., 2003). These fires

influenced forest composition, successional dynamics, and soil nutrients (Moore et al., 1999; Boerner et al., 2004; Weisberg, 2004; Blankenship and Arthur, 2006). Fire has been excluded from most North American ecosystems since ca. 1930, resulting in substantial changes in the structure and function of many forest types (Oberle, 1969; Moore et al., 1999; Brose et al., 2001). Fire exclusion has been linked to the accumulation of fuel loads and to successional dynamics disfavoring historically dominant species in many forests (Dodge, 1972; Covington and Moore, 1994; Brose et al., 2001; Schoennagel et al., 2004).

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In many deciduous forests of eastern North America, a lack of fire in the recent past is thought to have reduced regeneration and recruitment of oaks (*Quercus* spp.), which were a historically dominant species (Abrams, 1992; Brose et al., 2001; Shumway et al., 2001). Although oaks are still the dominant overstory tree, these forests exhibit a paucity of oak in the midstory and sapling layers, which are instead dominated by shade-tolerant and fire-sensitive species such as *Acer rubrum* L. and *A. saccharum* Marsh. (Lorimer, 1984; Abrams, 1992; Hutchinson et al., 2005; McEwan et al., 2005). This contrast in canopy dominance is thought to be part of an ongoing successional replacement of oak by maple (*Acer* spp.), and has been noted in many areas of the Eastern Deciduous Forest (Lorimer, 1984; Shotola et al., 1992; Abrams, 1998; McEwan and Muller, 2006). In order to impede this successional dynamic, and facilitate oak regeneration and recruitment, prescribed fire and silvicultural thinning have been applied in a variety of oak forests. An increasing body of evidence suggests that a combination of these two approaches (silvicultural manipulations and prescribed fire) is needed in order to impede oak-to-maple succession (Brose et al., 1999; Franklin et al., 2003; Albrecht and McCarthy, 2006).

In addition to their potential to modify successional patterns, prescribed burning and silvicultural thinning in forests have the potential to strongly influence forest carbon dynamics. Concern about the accumulation of atmospheric CO₂, and its potential role in global climate change, has led to the recognition that forests are exceedingly important as a global CO₂ sink (Lee et al., 2005). Furthermore, the Kyoto protocol (UNFCCC, 1998), which came into force on 16 February 2005, imposed emission ceilings on greenhouse gases for developed countries and adopted a cap-and-trade system that allows the trading of CO₂ equivalent emission credits (for Annex I countries, UNFCCC, 1998). Under the Kyoto framework, human-induced activities that lead to net changes in the carbon stock of terrestrial ecosystems should be added to, or subtracted from, the assigned emission standard (UNFCCC, 1998, Article 3). Thus, treatments that influence the carbon stored in forest trees, such as silvicultural manipulations and prescribed fire should be assessed to determine their influence on forest carbon storage.

The objectives of this study were (1) to assess the efficacy of prescribed fire and silvicultural thinning in facilitating oak recruitment and regeneration and (2) to examine the influence of these treatments on forest carbon storage and aboveground net primary production (ANPP). By dividing the forest stand into oak, maple, and other species, we examined the differential effects of restoration treatments on the mortality and recruitment of oak and maple species. We then categorized existing carbon stocks into living, cut, ingrowth, and dead sectors and quantified the transitions of carbon stocks between sectors following the restoration treatments. Further, we calculated the changes in ANPP (g C m⁻² year⁻¹) following treatments and examined whether ANPP was affected by thinning or burning. Lastly, we simulated the changes in ANPP following restoration treatments using the PnET-II forest carbon balance model (Aber et al., 1995) and compared the model output of ANPP with the field measurements.

2. Materials and methods

2.1. Site description and experimental design

This work was part of the Fire and Fire Surrogate (FFS) study, a project funded by the USDI-USDA Joint Fire Science Program that seeks to evaluate the efficacy of fire and silvicultural thinning (the fire “surrogate”) as restoration treatments in the major forest types of the United States (Stephens and Moghaddas, 2005; Apigian et al., 2006; Converse et al., 2006; FFS, 2006; Greenberg et al., 2006). Our work was conducted in the Ohio Hills FFS site, one of the 13 sites in an integrated research network utilizing a common experimental design (FFS, 2006). Each FFS site consists of three areas that serve as replicated blocks, each of which is divided into the following treatment units: (1) untreated control, (2) thinning, (3) thinning and prescribed burning, and (4) prescribed burning. This resulted in a total of 12 experimental units (3 blocks × 4 treatments). The area for each experimental unit ranges from 19 to 26.5 ha. Thinning was performed by commercial loggers and removed 5.6–10.1 m²/ha of the basal area while leaving the remaining crowns on the forest floor, and was completed in the winter of 2000–2001. This left a residual basal area of 18.1–22.6 m²/ha in the thinned treatment areas. The Ohio Department of Natural Resources, Division of Forestry conducted the prescribed burns, which were low to mid intensity ground fires (flame length <3 m in height) and were applied before leaf-out (between March 28 and April 5) in the spring of 2001 (Albrecht and McCarthy, 2006).

The following three areas made up the Ohio Hills FFS site: Tar Hollow State Forest (TAR; 39°20′00″N, 82°46′00″W), Raccoon Ecological Management Area (REMA; 39°12′00″N, 82°23′40″W), and Zaleski State Forest (ZAL; 39°21′20″N, 82°22′00″W). These sites are located in southern Ohio, on the unglaciated, maturely dissected Allegheny Plateau. Topography of the region is steep, with high hills and sharp ridges (Fenneman, 1938). The geology is predominantly sandstone, shale, and coals of the Pennsylvanian period, with narrow and scattered bands of limestone throughout (Boerner and Sutherland, 2003). Soils are dominated by the Shelocka–Brownsville complex sandy loams in TAR (Hamilton et al., 2003) and Steinsburg and Gilpin series silt loams in both REMA and ZAL (Lemaster and Gilmore, 1993). Forests are about 100 years since the last clearcut and currently dominated by *Quercus* (e.g., *Quercus prinus* L., *Q. alba* L., *Q. velutina* Lam., and *Q. coccinea* Muenchh.) and *Carya* spp. (*C. cordiformis*, *C. glabra*, *C. ovata*, and *C. tomentosa*) in the overstory (>10 cm DBH) and a mixture of *A. rubrum* L., *Nyssa sylvatica* Marsh., *Fagus grandifolia* Ehrh. in the midstory (Yaussy et al., 2003; Hutchinson et al., 2005). The understory tree seedlings (<140 cm tall) are largely comprised of *A. rubrum* L., *Sassafras albidum* (Nutt.) Nees, and *Quercus* spp. (Sutherland et al., 2003b; Albrecht and McCarthy, 2006). Regional climate is cool, temperate, and mesic with mean annual temperature of 11.3 °C and mean annual precipitation of 1024 mm (Sutherland et al., 2003a).

2.2. Measurements of aboveground carbon stocks and net primary production

The forest vegetation was measured within ten 50 m × 20 m (0.1 ha) permanent plots in each of the 12 experimental units by the research group at the USDA Forest Service Northern Research Station at Delaware, OH. Within each plot, all trees >10 cm DBH were marked and their diameter measured in the summer of 2000 (prior to any treatments), 2001, and 2002, and the dormant season of 2004. The impacts of the treatments on stems <10 cm DBH were published by Albrecht and McCarthy (2006) and therefore not included in this study. During each measurement, the status of each tree was categorized as living, cut, or dead. Additionally, in the years following the treatments, ingrowth (trees entering the >10 cm DBH size class for the first time) and mortality (newly dead trees >10 cm DBH) were documented, and then divided by the duration of each measurement interval to establish recruitment and mortality rates. Leaf litter was collected at the center of each plot using a 60 cm × 60 cm litter trap every 2 weeks in the fall (late September to mid November) of 2002–2004 and was then sorted into maple (*Acer* spp.), oak (*Quercus* spp.) and other (non-oak and non-maple species) before the dry weight was measured.

The aboveground biomass of each measured tree was estimated using allometric equations. With the exception of *Quercus muehlenbergii* Engelm., *S. albidum*, *Tilia americana* L., and *Ulmus americana* L., allometric equations were available in Jenkins et al. (2003). Allometric equations for *Q. alba* were used for *Q. muehlenbergii*. The equation for eastern hardwoods (Source ID: 140, Jenkins et al., 2003) was used for *S. albidum*, *T. americana*, and *U. americana*. The estimate of the aboveground biomass from each species was also grouped into maple (*Acer* spp.), oak (*Quercus* spp.) and other (non-oak and non-maple species). In addition to species, the selection of allometric equations was based on the DBH range for each equation. Thus, the aboveground biomass of most trees was estimated by more than one corresponding allometric equation. In such cases, the mean biomass outputs were used. Although allometric equations exhibited geographic specificity due to differential allocations to various organs, the estimations of aboveground biomass as a whole were similar between different equations (Fatemi, 2007). This is reflected by our low coefficient of variation (CV) among estimates from different allometric equations (mean CV = 11%).

The aboveground biomass increments were calculated by tracking the increments for each individual tree as follows (Clark et al., 2001):

$$\Delta\text{PLOTAGB} = \sum_{i=1}^n (\text{AGBT}_{2i} - \text{AGBT}_{1i}) + \sum_{j=1}^k (\text{IngAGB}_j - \text{AGBMIN}_j) \quad (1)$$

where $\Delta\text{PLOTAGB}$ is the plot-level aboveground biomass increment, AGBT_{2i} is the aboveground biomass of tree i at

the end of the measurement interval, AGBT_{1i} is the aboveground biomass of tree i at the beginning of the measurement interval, IngAGB_j is the aboveground biomass of the ingrowth tree j , and AGBMIN_j is the aboveground biomass of the ingrowth tree j when its DBH was 10 cm. The ANPP^* ($\text{g C m}^{-2} \text{ year}^{-1}$) was estimated by adding $\Delta\text{PLOTAGB}$ and the amount of foliar mass produced (FolMass ; g/m^2) between the end (T_2) and beginning (T_1) of the measurement interval:

$$\text{ANPP}^* = 0.5 \times \frac{\Delta\text{PLOTAGB} + \text{FolMass}}{T_2 - T_1} \quad (2)$$

The coefficient 0.5 in Eq. (2) was applied to convert the dry mass to carbon produced, assuming 50% of plant tissues were carbon (Brown et al., 1986; Hall and Uhlig, 1991; Marland and Schlamadinger, 1997; Penman et al., 2003). FolMass data were available only for ANPP^* measured between 2002 and 2004. FolMass for the other two intervals (2000–2001 and 2001–2002) were not measured and therefore estimated assuming constant ratio of foliar mass production and ANPP^* between different measurement intervals for each 50 m × 20 m plot:

$$\text{FolMass} = \text{ANPP}^* \times \frac{\text{FolMass}_{04}}{\text{ANPP}_{04}} \quad (3)$$

where FolMass_{04} ($\text{g C m}^{-2} \text{ year}^{-1}$) is the foliar production measured in the 2002–2004 interval and ANPP_{04} ($\text{g C m}^{-2} \text{ year}^{-1}$) is the ANPP^* measured in the 2002–2004 interval using Eq. (2). By combining Eqs. (2) and (3), Eq. (4) was derived to estimate the ANPP^* for 2000–2001 and 2001–2002 intervals:

$$\text{ANPP}^* = 0.5 \times \frac{\Delta\text{PLOTAGB}}{1 - 0.5 \times (\text{FolMass}_{04} / \text{ANPP}_{04})} \quad (4)$$

2.3. Leaf and wood phenology

Leaf budburst phenology of 10 mature trees for each of the 6 dominant taxa (*Q. alba*, *Q. velutina*, *Carya* spp., *Liriodendron tulipifera* L., *A. rubrum*, and *F. grandifolia*) was observed every 4–7 days from late March to mid May in 2004 and 2005 at the control stand of REMA site (Chiang and Brown, 2007). The date of budburst was determined for each tree when 50% of the buds had leaves recognizable through binoculars. To document periodic measurements of tree diameter growth, a band dendrometer (Keeland and Young, 2007) was also installed on each tree marked for the leaf phenology observation. Air temperature was recorded for each measurement to adjust for the thermal expansion of the band material (BAND-IT IDEX, Inc., Denver, CO). Total band length installed in each tree was calibrated to the length at 15 °C. Relative growth rate (RGR) of tree diameter was calculated as follows:

$$\text{RGR} = \frac{\text{Ln}(D_{t2}) - \text{Ln}(D_{t1})}{t_2 - t_1} \quad (5)$$

where D_{t2} and D_{t1} are the diameter measured using dendrometer at the end (t_2) and beginning (t_1), respectively, of one

measurement interval. The phenology of leaf budburst and tree diameter growth was used to parameterize PnET-II model.

2.4. PnET-II simulations

We then used PnET-II simulations to model forest carbon balance (Aber et al., 1995). Due to the difficulty in measuring the difference between net photosynthesis and respiration in a forested ecosystem, the field measurements of ANPP (ANPP*) are often based on a “bottom-up” approach, which estimates the accumulation of new organic matter over a period of time (Clark et al., 2001). In contrast, PnET-II is a process-based and physiological model that simulates the monthly balance of carbon and water in a forested ecosystem (Aber et al., 1995). The quantification of ANPP using PnET-II provided a top-down approach, which simulates the process of converting solar energy to organic matter under environmental constraints. Carbon uptake in the PnET-II model is based on a photosynthesis subroutine (Psn), which assesses potential photosynthesis rate ($A_{\max}$) by a linear function of leaf nitrogen content (N_{mass} ; %). Basal respiration is a constant fraction (default = 0.1) of $A_{\max}$. Potential gross photosynthesis ($1.1 \times A_{\max}$) is turned down as a function of the vapor pressure deficit effect of stomatal closure (DVPD) and deviation from optimum temperature for photosynthesis (DTemp). Day and night time temperature is applied in a Q_{10} (default $Q_{10} = 2$) function for the calculation of realized respiration rates. Within-canopy variation of photosynthesis rates are accounted for by changes in SLW along the vertical profile (50 layers) of the forest stand:

$$\text{SLW}_i = \text{SLW}_{\max} - \left(\text{SLW}_{\text{del}} \times \frac{\text{FolMassMax}}{50} \times i \right) \quad (6)$$

where SLW_i is SLW at i th layer ($i = 1\text{--}50$) of the canopy, $\text{SLW}_{\max}$ is SLW at the top of the canopy, SLW_{del} is the

amount of change in SLW_i with increasing foliar mass (g/m^2 ground area) above, and FolMassMax is the maximum foliar mass (g/m^2 ground area).

The other five subroutines of PnET-II include: *AtmEnviron*, *Phenology*, *WaterBal*, *SoilResp*, *AllocateMo*, and *AllocateYr*. *AtmEnviron* calculates vapor pressure deficit (VPD), day length, and growing degree days using monthly weather data. The *phenology* subroutine determines the date of leaf and wood growth by growing degree days. *WaterBal* calculates the water balance, including the level of water stress. Canopy gross photosynthesis is further adjusted in the *WaterBal* subroutine depending on the level of water stress. *SoilResp* calculates soil respiration rate as a function of mean monthly temperature. *AllocateMo* allocates net photosynthesis with the presence of DVPD, DTemp, and water stress to labile carbon pool and further to plant respiration, wood and root growth. At the end of each year, *AllocateYr* allocates the surplus carbon either to buds for the next year's foliar production or to wood for storage.

Some of our parameter inputs deviated from the model default (Table 1). Water holding capacity was estimated using empirical equations that described the relationships between soil texture and soil water characteristics (Saxton and Rawls, 2006). Leaf trait data (N_{mass} and SLW) were collected at the same sites (Chiang, 2007) because they are among the most sensitive variables in PnET simulations (Aber et al., 1996). The weighted means (weight = basal area) of N_{mass} and SLW for seven major canopy species: *A. rubrum*, *L. tulipifera*, *Carya* spp. (*C. cordiformis*, *C. glabra*, *C. ovata*, and *C. tomentosa*), *Q. alba*, *Q. coccinea*, *Q. prinus*, and *Q. velutina*, were used for PnET-II simulations (Chiang, 2007). SLW_{del} was calculated using Eq. (6), where SLW_{50} (SLW_i , $i = 50$) is the SLW at the crown bottom. The growing degree days (GDD) required for budburst, the end of leaf expansion, the beginning of wood growth, and the end of wood growth was obtained from the corresponding GDD for the date of each phenological event (Fig. 1). The day of year for the foliar senescence and maximum

Table 1
PnET-II parameters used in the simulation of thinning effects on aboveground net primary production (ANPP)

Variables	Control	Thinning 2001	Thinning 2002–2004
Latitude (°N)	39.28	39.28	39.28
Water holding capacity (cm)	16	16	16
N_{mass} (% mass)	1.96	1.96	1.96
SLW at crown top (g/m^2)	96.92	96.92	96.92
SLW at crown bottom (g/m^2) ^a	64.15	64.15	78.98
SLW_{del}	0.09	0.13	0.06
GDD required for budburst (degree days)	570	570	570
GDD required for the end of leaf expansion (degree days)	1400	1400	1400
GDD required for the beginning of wood growth (degree days)	500	500	500
GDD required for the end of wood growth (degree days)	3000	3000	3000
Senescence start (day of year)	284	284	284
FolMass (g/m^2 ground area)	354	248	309

Other inputs not included in the table were the same as the model default (Aber et al., 1995). The simulation of thinning effects on ANPP was performed at two stages. In the first stage (2001), leaf traits such as foliar nitrogen content (N_{mass}), specific leaf weight (SLW) at crown top and bottom, growing degree days (GDD) required for leaf and stem expansion, and the starting date of senescence remained unchanged under the thinning treatment. Due to the effect of thinning treatment, foliar mass (FolMass) was reduced by approximately 30% compared to that in the control site and the SLW_{del} was changed accordingly (see Eq. (6) in text). At the second stage (2002–2004), SLW at the crown bottom was increased as a result of thinning treatment while FolMass was recovered. Parameter inputs that were different from those under the control treatment were bold-faced.

^a SLW at crown bottom was not a required model input for PnET-II model. It was used to calculate SLW_{del} (see Eq. (6) in text).

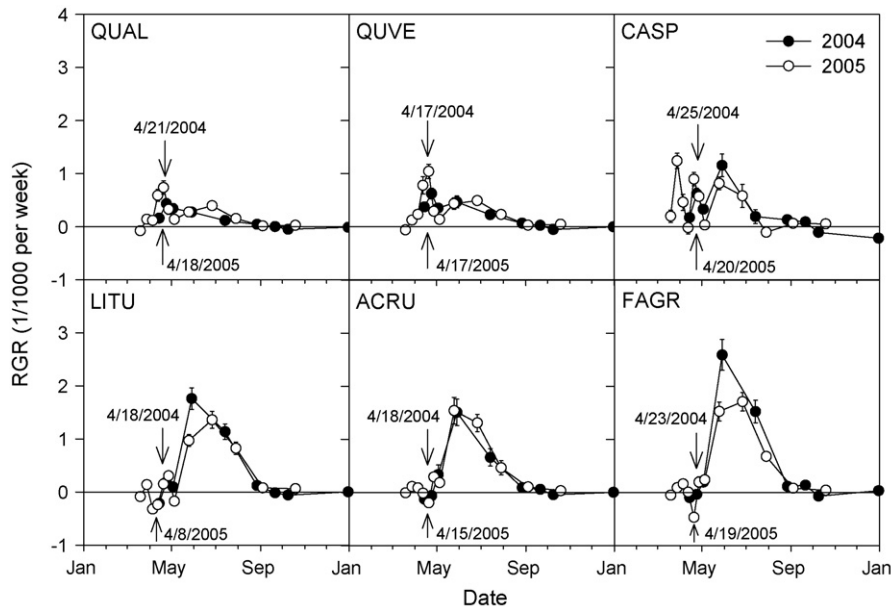


Fig. 1. The phenology of leaf budburst and stem diameter growth for *Quercus alba* (QUAL), *Quercus velutina* (QUVE), *Carya* spp. (CASP), *Liriodendron tulipifera* (LITU), *Acer rubrum* (ACRU), and *Fagus grandifolia* (FAGR) in a southeastern Ohio oak forest. The downward and upward arrows indicate the median date of budburst ($n = 10$) for each species. Both phenology data were observed/measured in the control stand of REMA site.

foliar mass were obtained from the leaf litter collection. The weather data required to run PnET-II (maximum and minimum temperature, precipitation, and photosynthetically active radiation) were obtained from the field weather station at the REMA site.

Prescribed burning had no significant effects on the leaf traits (Chiang, 2007); thus only the effect of silvicultural thinning on stand NPP was simulated. The effect of silvicultural thinning on the stand ANPP was simulated at two stages. At the first stage (2000–2001), we assumed leaf traits such as N_{mass} and SLW were predetermined in the previous growing season; thus, N_{mass} , SLW at crown top, and SLW at crown bottom were not susceptible to thinning treatments, which occurred in the dormant season between 2000 and 2001. Leaf traits (N_{mass} , SLW at crown top, and SLW at crown bottom) under the thinning treatment in 2001 were the same as those in the control site. At the same stage, maximum foliar mass was reduced by approximately 30% (from 354 to 248 g/m²) as a result of thinning and SLWdel was changed accordingly (see Eq. (6); Table 1). At the second stage (2002–2004), the SLW at the crown bottom was increased by approximately 23% while N_{mass} remained unchanged (Chiang, 2007). At the same stage, maximum foliar mass was recovered from 248 to 309 g/m² based on the leaf litter data (Table 1).

2.5. Statistical analysis

A mixed model, repeated measures analysis of variance was used to analyze the effects of thinning, burning, and time (year) on the changes in carbon stocks (living biomass, recruitment rate, and mortality rate) and ANPP* using the PROC MIXED routine in SAS (Littell et al., 1996; SAS Institute, 2001). Thinning and burning treatments were fixed factors and the three sites (REMA, ZAL, and TAR; replicated blocks) were

regarded as random effect. The design structure was a randomized complete block (RCB) design. The treatment structure was a two-way factorial design with repeated measures. The effects of burning (burn vs. no burn) and thinning (thin vs. no thin) were the between-subjects factors, which can vary only between subjects. The years of repeated measures (2001, 2002, and 2004) were regarded as within-subjects factors because measurements were applied to the same subject at different years. Stem density and aboveground biomass data were square root transformed while ANPP* data were either square root or hyperbolic arc sine transformed to achieve normality (D'Agostino Omnibus test, D'Agostino et al., 1990) and homogeneity of variance (Modified Levene Equal-Variance test, Hintze, 2006) prior to analysis.

3. Results

3.1. The phenology of leaf budburst and wood growth initiation

The relationship between the initiation of stem diameter growth and budburst was clearly different between ring-porous (*Q. alba*, *Q. velutina*, and *Carya* spp.) and diffuse-porous species (*L. tulipifera*, *A. rubrum*, and *F. grandifolia*) (Fig. 1). Ring-porous species consistently exhibited maximum stem growth (RGR) approximately coincident with leaf budburst (top row; Fig. 1). For instance, stem expansion in the two *Quercus* species began prior to leaf budburst and maximum RGR was attained simultaneous with leaf budburst. After the initial pulse of rapid growth, the RGR for oaks gradually declined through the rest of the growing season (Fig. 1). *Carya* species had dynamic growth prior to budburst, followed by a pulse of diameter growth from mid-May to August (Fig. 1). Diffuse-porous species exhibited substantially greater

maximum RGR, and these species attained maximum stem growth approximately 45–80 days after budburst (bottom row; Fig. 1).

3.2. Changes in stem density and aboveground carbon stocks after thinning and burning

Prior to the initiation of the thinning and burning treatments in our study sites, oak and maple constituted the majority of stem density. The living stem density on our study sites, prior to restoration treatments, was approximately 380 stems/ha (top row; Fig. 2), which we estimated to represent 233 Mg/ha ($Mg = 1 \times 10^6$ g) of aboveground biomass (top row; Fig. 3). Across all sites, oak and maple had similar stem density (top row; Fig. 2). Due to the generally larger size of oak trees in the study site, the living aboveground biomass was dominated by oaks (77%; top row in Fig. 3).

There were no differences in stem density or aboveground biomass (of the living stems) among the four treatment areas, for any of the species groups, prior to the initiation of the restoration treatments (top row; Figs. 2 and 3). Thinning removed, on the average, 130 stems/ha, which contained approximately 63,000 kg/ha of dry mass, and thus significantly ($P < 0.001$) reduced the living stem density and the aboveground biomass (second row; Figs. 2 and 3). Although a similar number of maple and oak stems (55 stems/ha; Fig. 2) were removed by the thinning operation, due to the generally large size of oaks, the dry mass of thinned stems from oaks was three times greater than that of maple species (second row; Fig. 3). The only significant effect of burning on living stems was to reduce the aboveground biomass of oaks ($P < 0.019$); oak density and the living stem density and biomass of maple and “other species” were not changed statistically by the treatment. After the thinning and burning treatments, the living stem

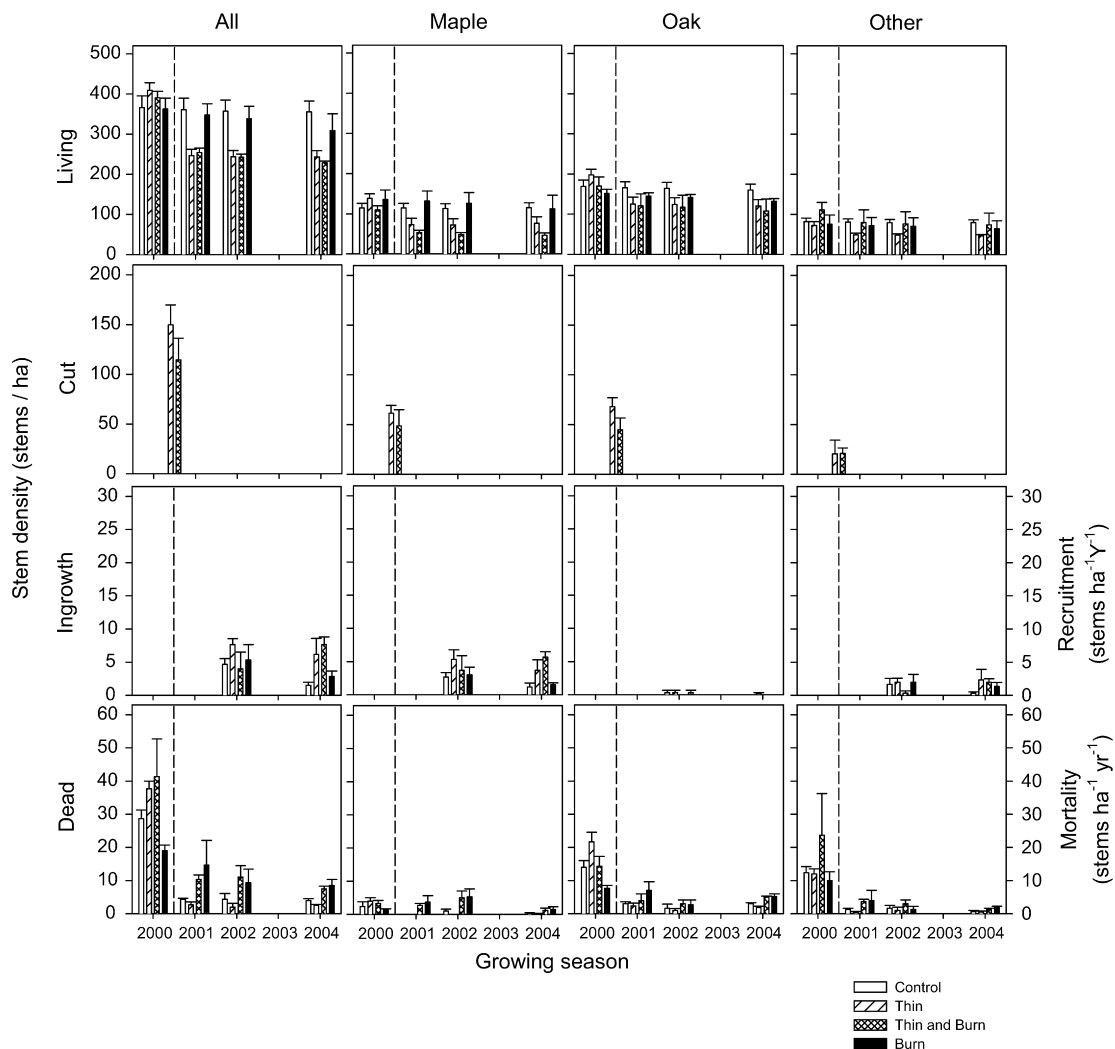


Fig. 2. Changes in stem density after silvicultural thinning and prescribed burning in oak forests of southeastern Ohio. Density is categorized by stems that were living, cut, ingrowth, and dead, before and after (separated by vertical dash lines) the restoration treatments (thinning and/or burning). Tree species were categorized into all species combined (All), *Acer* spp. (Maple), *Quercus* spp. (Oak) and non-maple and non-oak species (Other). Cut stems are those that were removed from the stand during the thinning treatments. The density of stems that grew into the >10 cm size class (ingrowth), and standing dead stems that were not previously recorded (dead) were normalized to per year basis, generating the recruitment rate and mortality rate (y-axis on the right), respectively. Data in 2003 were not measured and therefore not shown.

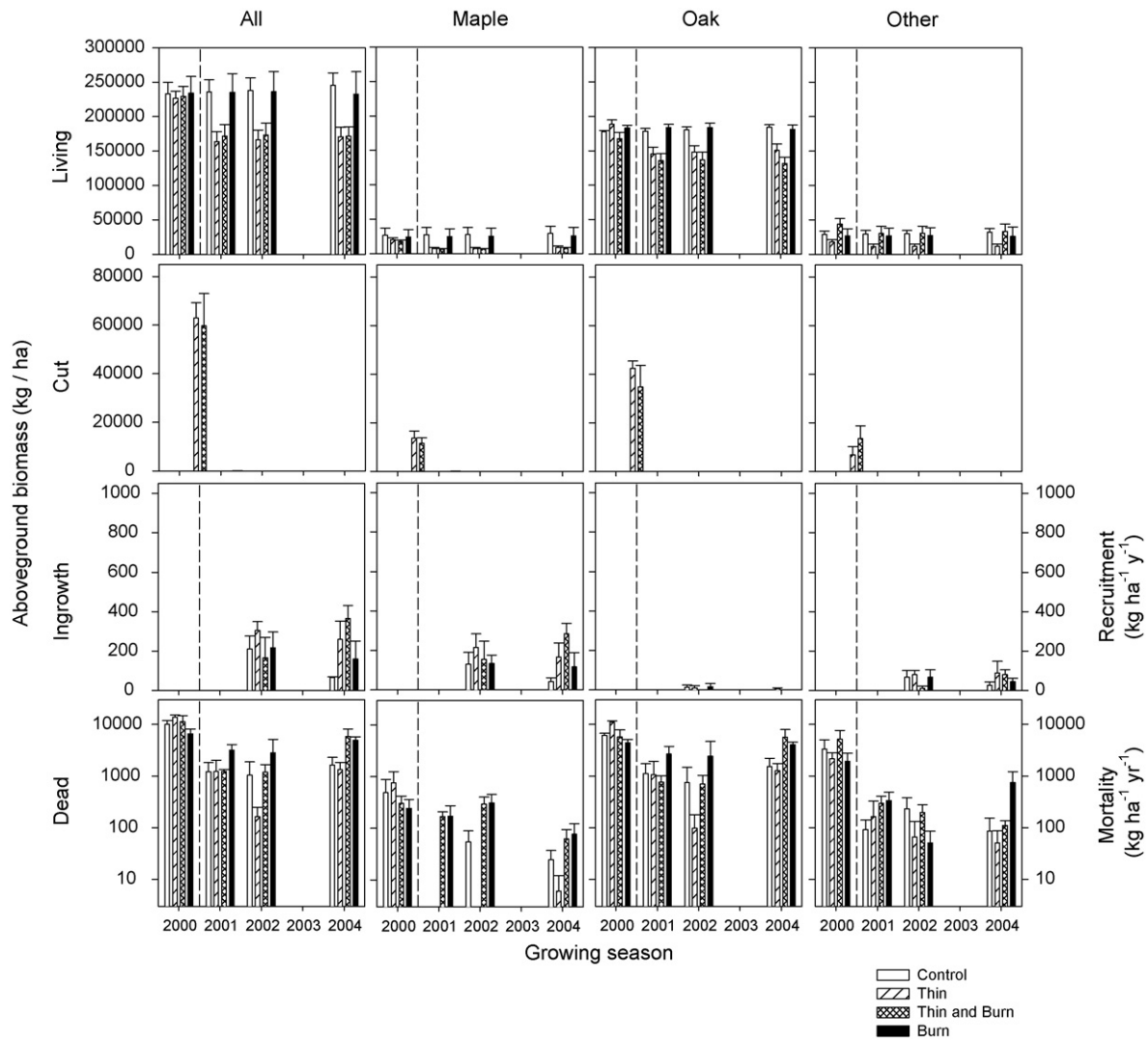


Fig. 3. Changes in aboveground biomass after silvicultural thinning and prescribed burning in oak forests of southeastern Ohio. Aboveground biomass is categorized by stems that were living, cut, ingrowth, and dead, before and after (separated by vertical dash lines) the restoration treatments (thinning and/or burning). Tree species were categorized into all species combined (All), *Acer* spp. (Maple), *Quercus* spp. (Oak) and non-maple and non-oak species (Other). Cut stems are those that were removed from the stand during the thinning treatments. The aboveground biomass of stems that grew into the >10 cm size class (ingrowth), and standing dead biomass that were not previously recorded (dead) were normalized to per year basis, generating the recruitment rate and mortality rate (y-axis on the right), respectively. Due to the wide range of aboveground biomass under the dead status, a LOG_{10} scale was used. Data in 2003 were not measured and therefore not shown.

density and aboveground biomass of all species groups did not exhibit significant yearly variation.

Thinning initiated substantial, species specific, pulses of recruitment into the >10 cm size class in 2002 and 2004 (third row; Figs. 2 and 3). Thinning significantly increased the recruitment of maples by both the number of stems (third row in Fig. 2; $P < 0.011$) and aboveground biomass (third row in Fig. 3; $P < 0.028$). The positive effect of thinning on maple recruitment was particularly pronounced in 2004 when recruitment of stems in areas treated with thinning was approximately three times greater than areas that had not been thinned (i.e., the control and burn treatments; third row in Figs. 2 and 3). The majority of recruitment stems were maple, or “other species”, while oak recruitment was minimal or absent. Oak recruitment was found in the control, thin, and burned sites in 2001 and the thinned site in 2004; however, oak

recruitment was <0.34 stems $\text{ha}^{-1} \text{year}^{-1}$ in all of these sites (third row; Fig. 2).

The mortality rate was highest in treatment areas that had experienced prescribed fire, and this trend was especially pronounced for oaks (bottom row; Figs. 2 and 3). Prior to the initiation of the restoration treatments, the density of standing dead trees was greater on the thinned treatment area than on either the control or burning treatment areas (bottom row; Fig. 2). Following the treatments, the density of standing dead stems (bottom row in Fig. 2; $P < 0.001$), and the aboveground biomass these stems represented (bottom row in Fig. 3; $P < 0.003$), was greatest in areas that had experienced prescribed burning. Both maples and oaks exhibited significant variation in mortality between years ($P < 0.050$), but they exhibited different trends in mortality rate (measured for years after treatments; bottom row in Figs. 2 and 3). The maple

mortality rate was relatively high in 2001 and 2002 for the areas that had been burned, but the mortality rate had decreased by 2004 (bottom row; Figs. 2 and 3). For oaks, the burn treatment resulted in the largest mortality rate of stem density in 2001 and 2004 and aboveground biomass in 2002 and 2004 (bottom row; Figs. 2 and 3).

3.3. Changes in ANPP after restoration treatments as predicted by field measurement

There was significant variation between growing seasons in the measured aboveground net primary productivity (ANPP*) of our study sites (Fig. 4; $P < 0.001$). In sites that were not thinned, ANPP* ranged from $560 \text{ g C m}^{-2} \text{ year}^{-1}$ in the 2000–2001 growing season to $340 \text{ g C m}^{-2} \text{ year}^{-1}$ in the 2001–2002 growing season (Fig. 4). Thinning, which removed approximately 30% of living aboveground biomass from the stand (Fig. 3), also substantially reduced the ANPP* (relative to other treatments) in the 2000–2001 growing season (Fig. 4). The loss in ANPP* as a result of thinning was temporary and there were no significant differences in ANPP* between restoration treatments in either the 2001–2002 or 2002–2004 measurement interval. This was reflected by a marginally significant interaction between thinning and year on overall ANPP*

($P < 0.061$) and significant interaction between thinning and year on the ANPP* of maple species ($P < 0.040$). In contrast, burning had no significant effect on the ANPP* of any species group.

3.4. Changes in ANPP after restoration treatments as predicted by PnET-II simulations

Model predictions (via PnET II; Table 1) suggested a similar temporal pattern to that from field measurements, but suggested higher ANPP than measured values. The predictions of ANPP from PnET-II ranged from $858 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2001 to $705 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2003, which were substantially higher than estimations from field measurements (Fig. 4). As was suggested by field measurements of ANPP (Fig. 4), the PnET-II simulations predicted a decline in ANPP the year following the thinning treatment (Fig. 5). The magnitude of the estimated decline (7%) was smaller than the decline predicted by field measurements (30%). In our simulations, leaf SLW at the mid to lower canopy, and the foliar biomass, were increased one year after the thinning treatment (Table 1). Under these conditions, the ANPP outputs were identical under thinned and control treatments from 2002 to 2004 (Fig. 5). Because PnET-II simulations are based on leaf traits, and previous work at the

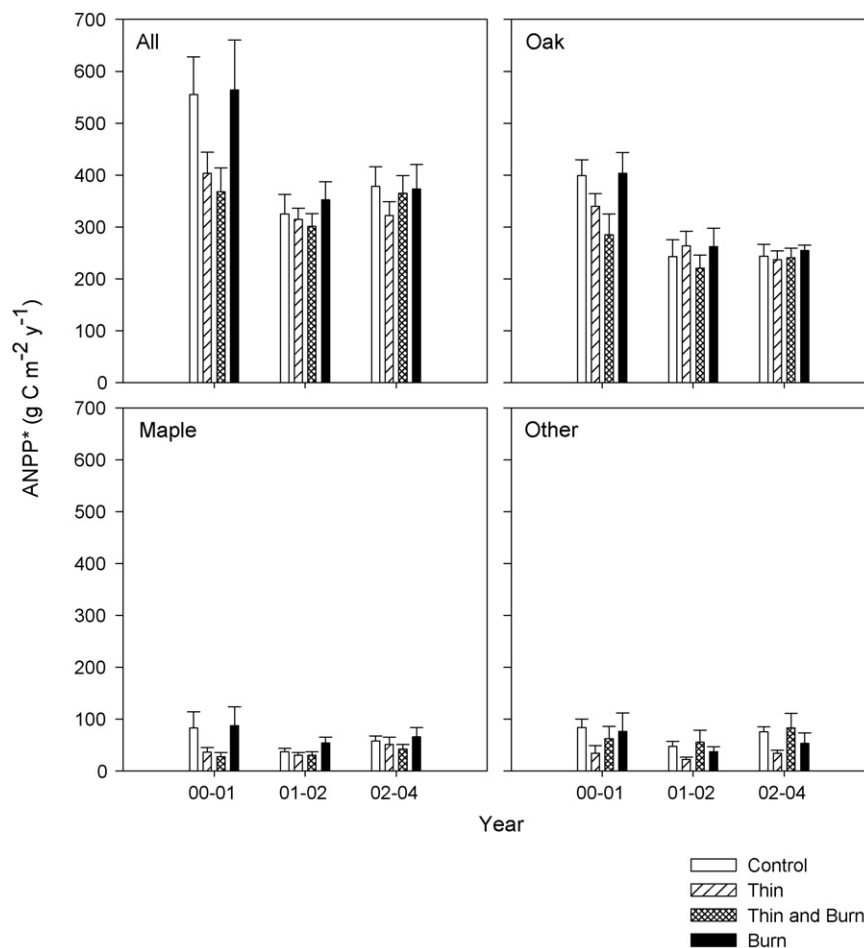


Fig. 4. Measured aboveground net primary production (ANPP*) of southeastern Ohio oak forests following prescribed fire and silvicultural thinning. Data were divided into the following categories: all tree species combined (All), *Quercus* spp. (Oak), *Acer* spp. (Maple), and non-oak and non-maple species combined (Other).

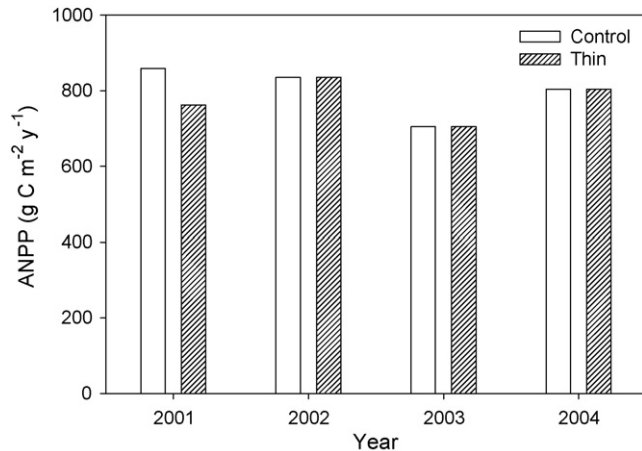


Fig. 5. PnET-II simulations of ANPP of southeastern Ohio oak forest under control and silvicultural thinning treatments.

study sites suggest fire does not influence these traits (Chiang, 2007), model simulations were not conducted for areas treated with prescribed fire.

4. Discussion

4.1. Silvicultural thinning and prescribed fire influence forest stem dynamics

Silvicultural thinning and prescribed fire are increasingly important forest management practices, particularly in ecosystems where historical disturbance regimes have been disrupted (Stephens, 1998; Moore et al., 1999; Washburn and Arthur, 2003). In oak forests of eastern North America, these treatments have been applied in order to impede maple succession and facilitate oak regeneration and recruitment (Arthur et al., 1998; Hutchinson et al., 2005; Albrecht and McCarthy, 2006). In our study, both thinning and burning treatments influenced forest dynamics, but it is unclear if they will drive the system toward the restoration objective. For instance, thinning initiated recruitment by maple stems in our study site, but recruitment of oak species was close to zero. This difference was probably due to the virtual absence of oak advanced regeneration in the midstory or sapling stratum of our study area, which is a pattern that has been documented in many other locations (Abrams, 1992, 1998; Hutchinson et al., 2005; McEwan et al., 2005). If the recruitment patterns noted in 2002 and 2004 remain constant, it will require approximately 15–30 years for the thinned stand to reach the pre-treatment level of stem density. Unlike pre-treatment conditions, however, the overstory of these future stands will almost certainly have a substantially increased maple component. These results support other findings (e.g., Albrecht and McCarthy, 2006) that suggest silvicultural thinning is only a viable option for oak restoration if it is coupled with other treatments that control oak competitors.

Prescribed fire in our study sites did not consume living trees ≥ 10 cm DBH, but still caused significant tree mortality. Oaks are generally considered fire resistant species (Abrams, 1992),

but in our study there was significant fire-related mortality of oaks. The sensitivity of oaks to prescribed burning in our study may have been related to the coincidence of diameter growth and the occurrence of prescribed fire. On our sites, prescribed fire was applied in spring when leaf buds were still dormant. Our data suggested that for ring-porous trees such as oaks, the initiation of stem growth was well before leaf budburst. Therefore, the period of spring stem growth in oaks should have coincided with the application of prescribed burning. In contrast, the initiation of stem growth in the diffuse-porous species (e.g., maples) was later than the date of leaf budburst, and thus well after the application of prescribed fire. It is probable that trees are more vulnerable to stem heating when the trees are breaking dormancy and initiating stem growth and this may be especially true for oaks, which have large, early wood vessels that are built early in the spring. If so, the timing of prescribed fire may have differentially disfavored oaks, despite their capacity to resist fire injury (Abrams, 1992). To increase the efficacy of prescribed burning for oak regeneration, forest managers should consider experimentally rescheduling the prescribed burning so that it is prior to, or well after, the period of stem growth for oaks.

4.2. Silvicultural thinning and prescribed fire influence forest carbon storage and ANPP

Forest management treatments such as thinning and burning have important implications for successional dynamics (Hutchinson et al., 2005; Albrecht and McCarthy, 2006; Blankenship and Arthur, 2006), but their influence on forest carbon storage and ANPP is not well understood. Forests in southern Ohio are among those with the highest biomass densities in the eastern United States (Brown et al., 1999). The aboveground biomass of the overstory trees (stems ≥ 10 cm DBH) estimated in this study was about 233 Mg/ha prior to thinning treatment. This value is larger than typical oak-hickory and maple-beech-birch forests (Schroeder et al., 1997), where aboveground biomass (DBH > 10 cm) ranged from 30 to 200 Mg/ha. Silvicultural thinning removed carbon in the form of biomass from the forest, much of which ostensibly ended up in long-term storage as building material (e.g., flooring). Compared to thinning, prescribed burning at this intensity (mostly ground fire) had no direct impact on the aboveground biomass of the overstory trees. Prescribed fire did increase stem mortality and, thus, may have resulted in the output of carbon from this ecosystem.

Our study demonstrated, using both field measurements and PnET-II simulations, that ANPP is negatively influenced by silvicultural thinning. Reducing overstory stem density through thinning caused a substantial reduction in ANPP in the year following the treatment. This decline in ANPP, though, did not persist beyond the first year as evidenced by both the field data and PnET-II simulations. Although thinning is associated with a decrease in canopy leaf mass, it also reduced shading and was associated with an increase in specific leaf weight (SLW) in the mid to low canopy positions. As simulated by the PnET-II model, ANPP recovered even though the stem density had been

reduced because of (1) an increase in subcanopy SLW and (2) a slight recovery of foliar mass in the canopy. Silvicultural thinning alters the light environment and thus drives alterations in canopy leaf traits, which have important roles in forest ANPP. Prescribed fire can influence forest carbon storage by removing understory vegetation and volatilizing stored carbon in forest fuels; however, the overstory ANPP was not affected by prescribed fire.

4.3. Comparison of field measurements and PnET-II simulations on ANPP

Although the PnET-II simulations and field measurements depicted similar patterns of decline and recovery of ANPP after thinning, there were some incongruities between the measured and modeled outputs. First, maximum ANPP estimates from PnET-II simulations were much larger than those from the field measurements. We hypothesize that this was due to the fact that trees <10 cm DBH were not quantified in our field measurements of biomass increments, but were modeled in the PnET-II simulations. Furthermore, even among the stems ≥ 10 cm DBH, there were potentially large unquantified organic components such as flowers, fruits, twigs, biogenic volatile organic compounds and leached organic matter (Clark et al., 2001). Second, the decline of ANPP following thinning was much larger in estimations derived from field measurements than from the PnET-II simulations. This may have been partially due to the differences in the time intervals for the two estimates of biomass production. PnET-II simulations followed the calendar year; however, due to the need to observe the crown vigor, the plot level biomass increments were measured between mid-summers of 2 years except in 2004 when measurements took place in the dormant season. Thus, the late summer biomass increments from trees remaining in the year after the thinning operation were not taken into account, which may have exaggerated estimates of ANPP decline. In addition, large variations of biomass increments during the summer can amplify estimations of yearly variation in ANPP. For example, diameter growth in July 2001 can be accounted in the increment for either 2000–2001 or 2001–2002 depending on the date of measurements. In future studies that seek to estimate ANPP, we suggest field measurements of biomass increments be made during the dormant seasons to avoid this potential problem.

5. Conclusions and management implications

Silvicultural thinning and prescribed burning have important implications for both successional dynamics and forest carbon storage. In this study, silvicultural thinning created recruitment opportunities, but these were captured by maple stems while oak recruitment was minimal. Thinning removed carbon from the stand (in the form of removed logs) and also resulted in a substantial, but temporary, reduction in ANPP. The reduction of ANPP by thinning lasted only 1 year, and its recovery was likely due to changes in foliar mass and leaf traits. Prescribed fire did not influence the ongoing carbon uptake as measured by ANPP, but it did cause significant

mortality. The increased mortality of oaks may have been partially due to the fact that fire was applied during the initiation of stem growth in oak species. Forest managers whose goal is to impede maple succession and promote oak recruitment through prescribed burning should consider the phenological differences between oaks and maples and alter the timing of burning accordingly.

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