

Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests

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Abstract

Second-growth oak forests in the central hardwoods region are considered compositionally unstable in the absence of large-scale disturbances. While prescribed burning and mechanical thinning treatments are potential options for managing succession in mixed-oak forests, few studies have adequately studied tree successional patterns in mature (>100-year old) stands following application of these anthropogenic disturbances. In a randomized block factorial design, we studied tree recruitment patterns (stems <10 cm dbh) in three mature southern Ohio forests that contained stands divided into four treatment units (each approximately 30 ha): control, prescribed fire, mechanical thinning, and mechanical thinning followed by prescribed fire. Treatments were applied in the dormant season of 2001. A single prescribed fire reduced seedling and sapling densities of *Acer rubrum*, the understory dominant in these forests. *A. rubrum* rapidly recovered to pre-treatment levels in all treatment units four growing seasons following the disturbances, largely by colonizing from seed and resprouting from top-killed sapling regeneration. Mechanical thinning treatments accelerated understory recruitment of early-successional, shade-intolerant tree species that regenerated from seed (e.g., *Liriodendron tulipifera*) and resprouted from a seedling bank (e.g., *Sassafras albidum*). Oak (*Quercus* spp.) seedlings <140 cm tall densities were unresponsive to all treatments over the 4-year study period, although densities were dynamic through time. Seedling densities of *Q. alba* and *Q. prinus* declined in all treatments over the 4-year study period, while seedling densities of *Q. velutina* increased in all treatments. Oak seedling sprouts were not released from growth suppression in silviculturally thinned or burned forests. Four growing seasons following treatment application, oak regeneration remained at a competitive disadvantage with high densities of early-successional species present in xeric and intermediately moist portions of thinned stands. To maintain adequate oak recruitment in these forests, our data suggest that prescribed fire may need to be applied several years following a mechanical thinning treatment. Periodic fires are predicted to control the strong resprouting response of *A. rubrum* and fast-growing opportunistic tree species.

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1. Introduction

The successional transition of oak (*Quercus*) forests to mesophytic dominated systems is a geographically widespread phenomenon in the Central Hardwood Region (McCarthy et al., 1987; Crow, 1988; Cho and Boerner, 1991; Lorimer, 1993; Goebel and Hix, 1997). Correlative data suggest that periodic surface fires were a key ecosystem process that structured historical and contemporary eastern oak dominated systems (Abrams, 1992). The fire and oak hypothesis has been used to explain a correlation between the increasing abundance of

shade-tolerant species in contemporary forests and concurrent decline in oak abundance, with the onset of region-wide fire-suppression policies ca. 70 YBP (Crow, 1988; Abrams, 1992; Brose et al., 2001).

Witness tree data from the southern Ohio landscape indicate that contemporary oak forests contain greater densities of shade-tolerant (fire-sensitive) trees compared to forest communities at the time of Euro-American settlement (Dyer, 2001). An open-park-like structure and lack of fire-intolerant vegetation noted by early Euro-American settlers in this region (Hutchinson et al., 2003a) provides additional evidence that periodic surface fires may have been important in these forests prior to Euro-American settlement (Day, 1953; Pyne, 1982; Williams, 1989).

Contemporary second-growth mixed-oak forests in southern Ohio developed following broad-scale land-clearing activities

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associated with the charcoal iron industry. A typical coal furnace utilized up to 250 ha of regional forest on an annual basis (Hutchinson et al., 2003a). Based on historical records, 60% of forests in many sections of southeastern Ohio were clearcut down to 10 cm diameter trees between 1850 and 1860. Low- to moderate-intensity surface fires were common during this period; dendrochronological data from local hardwood stands indicate a median fire return interval of <5 years in local forests, until effective fire-suppression policies began in 1932 (Sutherland, 1997; McCarthy et al., 2001; Sutherland and Hutchinson, 2003). Post-settlement fires in southern Ohio predominantly occurred in the dormant season, the period of tree cambium inactivity (Sutherland, 1997).

Regional forest recovery began following the decline of timber-based industries at the turn of the 20th century. Many forest stands are currently in the understory reinitiation stage of development and contain dense understories of *A. rubrum* and late-successional, shade-tolerant species (Goebel and Hix, 1996; Hix and Percy, 1997; Small and McCarthy, 2002). Previous studies indicate that this dense, shade-tolerant regeneration layer beneath oak canopies suppresses the life-history transition of oak seedlings (Lorimer, 1993; Lorimer et al., 1994). Consequently, oak saplings are often poorly represented in these mixed-oak forest communities despite a moderate abundance of oak seedlings in the understory (McCarthy et al., 1987; Goebel and Hix, 1996; Hutchinson et al., 2003b). Moderately shade-tolerant oak seedlings occupying closed-canopy forests of this region are unable to recruit into larger size classes and capture tree-fall gaps (Cho and Boerner, 1991; Goebel and Hix, 1997), instead they often persist for many decades in a 'seedling sprout' life-stage via reoccurring dieback and resprout cycle (Merz and Boyce, 1956).

Many eastern oak forest systems may be transitional communities in the absence of canopy-reducing disturbances (Carvell and Tryon, 1961; Brose et al., 1999). However, without human intervention large-scale disturbances such as catastrophic blowdowns are uncommon in the southern Ohio landscape (Runkle, 1990). Ice-storms occasionally modify canopy structure, although damage is often concentrated on lower slopes and valley floors (Boerner et al., 1988) where oak regeneration naturally occurs at low densities and competes poorly in these highly productive environments (Kolb et al., 1990). Pre-settlement canopy altering disturbances caused by passenger pigeon (*Ectopistes migratorius*) roosting activity may have reduced canopy densities in central hardwood forests at magnitudes ranging from mid-sized gaps to stand-initiating disturbance events (Ellsworth and McComb, 2003). Ellsworth and McComb (2003) suggested that the formation of large canopy openings simultaneously increased fuel loads which may have facilitated moderately intense fires that favored light demanding and fire resilient eastern oak species. In mixed-oak forests of the Virginia Piedmont Region, Brose et al. (1999) demonstrated that a shelterwood harvest that removed 50% of the basal area followed by an intense spring fire 2–4 years later was successful at regenerating oak. They hypothesized that this dual disturbance mimics the historic disturbance regimes that

maintained upland oak-dominated stands over the last 3–4 millenia (Brose et al., 2001).

Prescribed burning and silvicultural thinning treatments are increasingly used to manage succession in central hardwood oak forests. Yet, few well replicated experimental studies have examined forest successional patterns in mature (>100-year old) forests following the application of these anthropogenic disturbances (Brose, 1999; Franklin et al., 2003). We investigated tree recruitment patterns using a fully replicated experimental block design across the southern Ohio landscape. As part of an ecosystem-scale management project, we sampled three forest blocks each consisting of four treatment units: untreated control, prescribed surface fire treatment, canopy thinning treatment, and canopy thinning followed by a prescribed surface fire treatment (each treated stand ca. 20–30 ha). In permanent plots distributed along a topographic moisture–fertility gradient, we evaluated the structural and compositional dynamics of tree regeneration (<10 cm, diameter at breast height, dbh) over a 5-year period. We sought to answer the following questions: (1) Do these anthropogenic disturbances alter forest successional patterns in 100-year-old central hardwood forests? (2) Does the competitive status of oak regeneration improve with thinning and/or burning activities? (3) Do the resultant changes in forest structure favor oak recruitment?

2. Study area

The USDA Forest Service Fire and Fire Surrogate (FFS) research project is a long-term study that explores potential management choices for restoring forest ecosystems where surface fires have been excluded for decades (<http://www.fs.fed.us/ffs>). The FFS study sites located in southern Ohio are representative of second-growth mixed-oak forests throughout the central hardwood region: Tar Hollow State Forest (39°33'0"N, 82°76'7"W), Vinton Furnace Experimental Forest (39°20'0"N, 82°39'0"W), and Zaleski State Forest (39°35'5"N; 82°37'0"W). Each forest site (statistical block) is located in the unglaciated Allegheny Plateau physiographic province of southeastern Ohio (Fenneman, 1938), and is currently in the understory reinitiation stage of development (Oliver and Larson, 1996). *Quercus* spp. represents >80% of the basal area of canopy (>10 cm dbh) trees at these sites. Relative abundances based on pre-treatment data collected at the sites indicate that the sapling stratum (>140 cm tall, <3 cm dbh) is dominated by shade-tolerant species: *Acer rubrum* L. (37%), *Nyssa sylvatica* Marsh. (25%), *A. saccharum* Marshall (15%), *Fagus grandifolia* Ehrh. (13%) and *Oxydendrum arboreum* (L.) DC (10%). The tree seedling stratum (<140 cm tall) is comprised of: *A. rubrum* L. (64%), *Sassafras albidum* (Nutt.) Nees (13%), *Q. prinus* L. (9%), *Q. alba* L. (5%), *Q. sub. Erythrobalanus* (5%), *N. sylvatica* (2%), and *O. arboreum* (2%). Nomenclature follows Gleason and Cronquist (1991).

Forests in southern Ohio have been heavily impacted by human activities. Besides the massive forest clearance in the 1800s, other important regional disturbances include the extirpation of the passenger pigeon, loss of *Castanea dentata*

(Marshall) Borkh. (American chestnut) from the canopy in upland areas, and the near extirpation of important game such as wild turkey (*Meleagris gallopavo*) and white-tail deer (*Oidocoileus virginianus* (Boddaert)). Wildlife populations have since rebounded. White-tail deer herd densities presently range between 5 and 6 deer/km² in southeastern Ohio (Apsley and McCarthy, 2004). At these comparatively low densities deer are not browsing tree regeneration at frequencies great enough to significantly alter forest structure and composition (Apsley and McCarthy, 2004).

Braun (1950) classified this area as the Low Hills Belt component of the mixed mesophytic region with *Quercus* (oak), *Carya* (hickory), and *F. grandifolia* (beech) dominating the upland second-growth forests. This region is characterized by a highly dissected topography (approximately 100 m total relief) that generates strong microclimatic gradients resulting in dry west-, and south-facing slopes, and more mesic north- and east-facing slopes (Wolf et al., 1949). Average monthly temperature ranges from -2°C in January to 22.6°C in July (NOAA, 2003). Average annual precipitation is 100.6 cm and is distributed evenly throughout the year.

3. Methods

3.1. Treatments

Following collection of pre-treatment data (summer 2000), stands receiving thinning treatments were commercially thinned from below in the winter of 2000–2001. Primary skidder trails were constructed on the ridgetops and secondary skidder trails divided off the primary ones. At each site, the thinning treatments reduced stand basal area by 20–30% (Table 1), leaving a large number of seed-producing residual oaks in the overstory and creating a gap mosaic stand structure. Crowns of cut trees were left remaining on the forest floor.

Forest floor disturbances were largely isolated to skidder trails and loading pads.

Prescribed burns were conducted during the spring fire season (March–April, 2001), just prior to leaf-out. Local meteorological conditions at ignition time were within the boundaries of burn prescriptions for the state of Ohio. Fires were heterogeneous within and across sites, but flame lengths rarely exceeded 2 m in height. Based on fire behavior data collected at geo-referenced gridpoints from all study sites, the mean rates of spread ranged from 6.2 to 11.3 m/min (Iverson et al., 2004b). Fires consumed unconsolidated leaf litter while 1-h woody fuels were occasionally consumed. Across all sites, fires in the burn treatment exhibited slightly greater coverage (area burned) and intensity than the thin + burn treatments because the skidder trails and uncured slash interrupted the spread of fire across thinned stands (Iverson et al., 2004a). For a more complete description of fire behavior, see Iverson et al. (2004b).

3.2. Field sampling

We studied tree regeneration (<10 cm dbh) at three study areas (statistical blocks) each containing the following experimental treatments (stands): control, thinning treatment (thin), a prescribed burn treatment (burn), and a combination of thinning and burning treatment (thin + burn). Stand size varied across study areas and ranged from 21 to 30 ha but each treatment included the full range of topographic relief. Tree regeneration was sub-sampled in ten 0.1 ha (50 m × 20 m) permanent vegetation plots per treatment (a total of 40 plots/site; 120 plots in the landscape) in summer 2000 (pre-treatment), and then again in summer 2001 (first post-treatment sample) and summer 2004 (second post-treatment sample). Vegetation plots in each treatment were stratified along an integrated moisture index (IMI), which uses landscape features (slope–aspect shading index, cumulative flow of water

Table 1
Oak and maple abundance (trees >10 cm dbh) of six mixed-oak forest stands before (2000) and after (2001) silvicultural thinning treatments

	REMA		Tar hollow		Zaleski	
	T	TB	T	TB	T	TB
Basal area (m ² /ha)						
Oak before	20.9	18.0	24.1	21.7	22.6	20.5
Oak after	16.6	15.6	18.3	15.3	16.2	16.1
Red maple before	2.7	1.3	1.9	1.7	3.7	3.0
Red maple after	1.05	0.7	0.6	0.4	1.5	0.8
Total before	27.4	28.0	31.7	32.6	27.6	25.5
Total after	19.1	22.6	22.0	20.9	18.8	18.4
Density (stems/ha)						
Oak before	226	120	144	142	224	257
Oak after	146	95	93	88	147	194
Red maple before	105	49	60	35	176	148
Red maple after	48	32	33	19	104	66
Total before	441	372	341	351	446	447
Total after	256	297	227	246	294	292

T, thinning treatment; TB, thin + burn treatment.

downslope, curvature of the landscape, and water-holding capacity of the soil) and topographic data with GIS to predict local soil moisture and fertility conditions (Iverson et al., 1997).

Tree seedlings were sampled in 20 permanent 1 m² quadrats nested within each 0.1 ha vegetation plot. We recorded each tree seedling into one of two seedling size classes based on height: small (≤ 50 cm) or large (50.1–140 cm). Woody saplings and shrubs were sampled in three permanent 0.01 ha (10 × 10 m) subplots nested within each 0.1 ha vegetation plot. For all shrubs >1 m in height, cover was visually estimated as the percentage of plot area covered from a vertical projection. Saplings included all stems >140 cm tall and were tallied based on the following dbh size classes: small (<3 cm) and large (3–10 cm). In the 2004 field sampling effort, stems >140 cm tall were placed into one of three regeneration classes: basal sprout from tree <10 cm dbh, >140 cm ht, basal sprout from felled tree >10 cm dbh, and other (i.e., stems not originating as basal sprouts from trees >140 cm ht). The latter class included residual stems that survived the treatment, and stems that recruited into the sapling stratum by seed or seedling sprout.

3.3. Data analysis

For all subsequent analyses of stem densities we summed the twenty 1 m² seedling quadrats (seedling stratum) and three 100 m² sapling subplots (sapling stratum) in each 0.1 ha vegetation plot ($n = 30$ plots per treatment). Each 0.1 ha vegetation plot in the landscape was classified into one of three IMI classes based on the raw IMI values: xeric (IMI < 35), intermediate (IMI = 35–50), and mesic (IMI > 50). The distribution of plots by IMI class was uneven among the treatments; however, all treatments contained at least 5 and no more than 16 plots in each IMI class.

To determine treatment effects on forest understory structure, tree regeneration densities in each of four size classes (two seedling size classes and two sapling size classes) and shrub cover per 0.03 ha plot was analyzed separately in a randomized complete block (RCB) mixed-model (PROC MIXED) analysis of covariance (ANCOVA) (SAS Institute, 2001). Forest sites were considered blocks (random effect), with treatments and IMI as the independent factors (fixed effects). Plots, the experimental unit, were considered a repeated effect in the model since they were permanent and sampled at three different time intervals. To more accurately assess treatment effects, pre-treatment (baseline) data were used as the covariate. Information criteria was used to select the covariance model that provided the best fit of each modeled dataset; the covariance model with the lowest Akaike Information Criterion (AIC) was used to avoid committing a type 1 error (Littell et al., 2002). When the treatment × year interaction was significant, a posteriori least-squares mean separation with Bonferroni correction ($\alpha = \alpha/k$) was used to test for differences among treatments and years. Tree densities were square-root transformed to improve normality and homogeneity of variance prior to the analysis.

For the dominant overstory (*Carya* spp., *Quercus alba*, *Quercus prinus*, and *Quercus velutina*) and understory (*A.*

rubrum, *L. tulipifera*, *N. sylvatica*, and *S. albidum*) tree species we formed two size classes (seedlings <140 cm tall, and saplings >140 cm tall, but <10 cm dbh) and analyzed regeneration density changes in each size class separately with the aforementioned mixed-model RCB ANCOVA. For the 2004 dataset, a log-linear analysis was used to determine if the number of sapling stems in each regeneration class was independent of the treatments.

Do anthropogenic disturbances significantly alter forest successional patterns? To address this question, we used a recently developed modification of redundancy analysis (RDA). Traditional canonical RDA preserves the Euclidean distances among sites, making analysis of a species × site matrix with a large number of zeroes inappropriate. However, Legendre and Gallagher (2001) proposed that with the proper transformation of a species × site matrix containing raw species abundances, a transformed symmetrical matrix of distances can be used directly in Euclidean distance based methods (e.g., PCA and RDA). This permits the testing of relationships among experimental factors and species abundances (i.e., multivariate response variable) in an ANOVA-like factorial design, and the construction of ordination bi-plots depicting the relationships of species with experimental factors (or environmental variables) in Euclidean space. Permutation tests can be used for significance testing of the main factors and their interactions, thereby circumventing the multivariate normality assumption inherently violated with species compositional data matrices containing numerous zeroes.

We performed separate RDAs with three experimental factors (treatment, IMI, and year) for each of the four tree regeneration size classes (or four site × species matrices). First, tree species that occurred in <5% of the sample units (McCune and Grace, 2002) were removed prior to applying the Hellinger distance transformation to each species × site matrix. In previous studies with community compositional datasets, the Hellinger transformation provided the best representation of sample units in Euclidean space (Legendre and Gallagher, 2001). Second, we constructed an environmental matrix in which each of the experimental factors and blocks was coded as a ‘dummy’ variable (ter Braak and Smilauer, 2002). The transformed species × site symmetrical matrix of distances was used as the multivariate response variable in a three-way ANOVA model. Each factor was tested separately while other factors were considered covariables in the analysis (partial canonical analysis, Legendre and Legendre, 1998); forest sites were considered blocks in each model. Significance tests for each factor and their interactions were performed using 499 Monte-Carlo permutations; permutations were restricted by a split-plot design and within-block permutation structure (ter Braak and Smilauer, 2002).

4. Results

4.1. Forest understory structure

Densities in each of the four regeneration size classes exhibited significant treatment effects (all P -values < 0.0001)

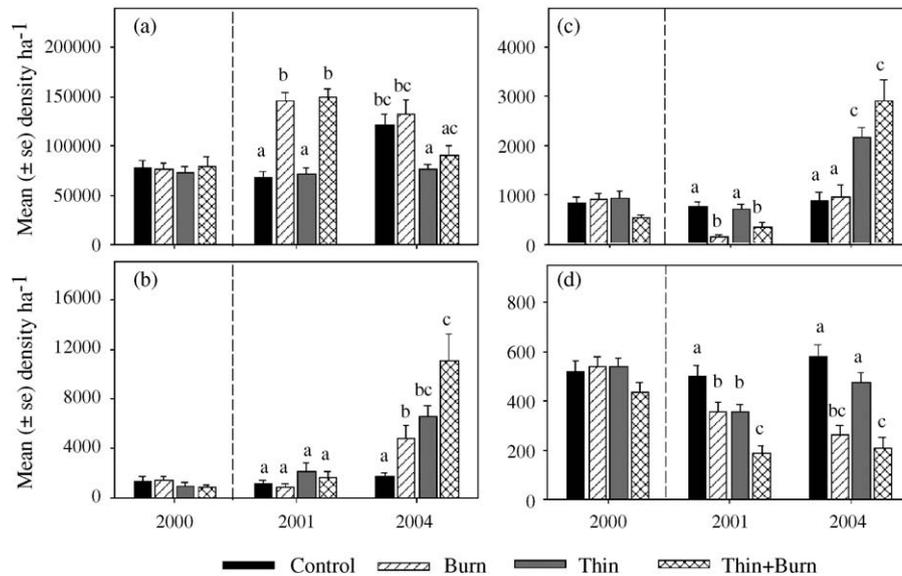


Fig. 1. Mean (\pm 1 S.E.) densities of tree regeneration among treatments and years. Treatment \times year interactions were significant for each size class in a mixed-model ANCOVA, with pre-treatment densities serving as the covariate. Bars with different letters are significantly different according to post hoc multiple comparison of LS-means with Bonferroni adjusted P -values. *Seedlings*: (a) small, <50 cm tall; (b) large, 50–140 cm tall; *saplings*: (c) small, <3 cm dbh; (d) large, 3–10 cm dbh.

and treatment \times year interactions (all P -values < 0.0001). While the treatment response of large seedlings was delayed until 2004, the density of small seedlings increased two-fold following the burn and thin + burn treatments in 2001 (Fig. 1a and b). Rapid density increases in small seedlings occurred because of extensive sprouting following top-kill of root-suckering species (e.g., *Sassafras albidum* and *N. sylvatica*), while the consumption of leaf litter stimulated germination of the seed banking *Liriodendron tulipifera*. Small seedlings also exhibited significant treatment \times IMI ($P = 0.03$) and IMI \times year interactions (14.56, $P < 0.0001$) but an insignificant treatment \times IMI \times year interaction ($P = 0.45$). Whereas no differences were observed among IMI classes in 2001, small seedling densities in 2004 were greater on xeric (113,445 stems/ha) and intermediate plots (123,455 stems/ha) than mesic plots (76,605 stems/ha). Small seedling densities in the control and burn treatment were also greater on xeric plots (140,000–141,000 stems/ha) than mesic plots (78,000–80,000 stems/ha) in 2004; however, small seedling densities were uniformly distributed among IMI classes in the thin and thin + burn treatments through time. Although no treatment differences were observed the first-growing season following treatment application, large seedling densities increased significantly in all treatments by 2004 (Fig. 1b). A combination of fire and thinning accelerated recruitment of large seedlings at greater rates than either burning or thinning alone (Fig. 1b). Large seedling densities were consistently distributed along the moisture gradient (IMI effects and IMI interactions: all P -values > 0.09).

Small-diameter (>140 cm ht to <3 cm dbh) and large-diameter (3–10 cm dbh) sapling densities declined immediately following fire (Fig. 1c and d). However, four growing seasons following a single surface fire, small-diameter saplings recovered to pre-treatment density levels whereas densities in

the thin and thin + burn treatments exceeded pre-treatment levels (Fig. 1c). Small-diameter sapling re-establishment, however, was not consistent along the moisture gradient (IMI \times year: 4.37, $P < 0.015$); recruitment was greater on xeric plots (2304 stems/ha) relative to mesic (1295 stems/ha) and intermediate (1625 stems/ha) plots. In contrast, large-diameter sapling densities initially reduced by fire never recovered in the burn and thin + burn treatment, where densities remained below 200 stems/ha in 2004 (Fig. 1d). Fire also interacted with the moisture gradient (treatment \times IMI: $P = 0.04$), whereby large-diameter sapling densities were greater on mesic plots (thin + burn: 290 stems/ha; burn: 380 stems/ha) than on intermediate (thin + burn: 140 stems/ha; burn: 281 stems/ha) and xeric plots (thin + burn: 165 stems/ha; burn: 256 stems/ha). There were no significant IMI \times year \times treatment interactions for either sapling size class (P -values > 0.08).

Shrub/vine cover exhibited significant treatment ($P < 0.0001$) and treatment \times year effects ($P < 0.0001$). The first-growing season following prescribed fire, shrub/vine cover was significantly lower in the burn and thin + burn treatment compared to the control and thin treatment (Table 2). By 2004, however, shrub cover increased significantly in the thinning treatments but remained stable in the burn only treatment. The dominant shrub taxa, *Smilax rotundifolia* and *Rubus* spp., also showed significant treatment (*Smilax*: $P < 0.0001$; *Rubus*: $P < 0.0001$) and treatment \times year (*Smilax*: $P = 0.02$; *Rubus*: $P < 0.0001$) effects. Three growing seasons following top-kill by fire (2004), *Smilax* never rebounded in the burn and thin + burn treatments where cover remained significantly lower than control plots (Table 2). *Smilax* was also less responsive to the thinning treatments than *Rubus*; *Rubus* averaged 8% cover in thin and thin + burn plots by 2004, though it was mostly absent from these plots prior to the

Table 2
Mean (\pm 1S.E.) percent cover (per 0.03 ha) of the shrub/vine stratum among the treatments

Treatment	<i>Rubus</i> spp.	<i>Smilax rotundifolia</i>	Total shrub/vine cover
Control			
2001	0.7 \pm 0.7 ^a	10.9 \pm 4.7 ^a	15.3 \pm 5.5 ^{ac}
2004	1.2 \pm 1.2 ^a	8.1 \pm 3.4 ^a	11.4 \pm 4.6 ^{ac}
Burn			
2001	0.0 \pm 0.0 ^a	0.7 \pm 0.4 ^b	1.2 \pm 0.6 ^b
2004	0.3 \pm 0.2 ^a	1.1 \pm 0.2 ^b	1.5 \pm 0.3 ^b
Thin			
2001	0.03 \pm 0.03 ^a	3.1 \pm 0.9 ^c	6.6 \pm 2.2 ^a
2004	7.8 \pm 2.2 ^b	6.0 \pm 1.8 ^{ac}	19.4 \pm 5.6 ^c
Thin + burn			
2001	0.0 \pm 0.0 ^a	0.7 \pm 0.2 ^b	1.5 \pm 0.4 ^b
2004	8.0 \pm 3.0 ^b	1.9 \pm 0.6 ^b	19.6 \pm 5.9 ^{ac}

Pre-treatment (2000) data were used as a covariate in a mixed-effects ANCOVA model to test for differences among treatments. Means within a column without the same letter are significantly different ($P < 0.05$) according to Bonferonni adjusted P -values (LS-means).

treatments (Table 2). There were no significant IMI effects or IMI interactions on the dominant shrub/vine taxa and total shrub/vine cover (all P -values > 0.06).

4.2. Community compositional patterns and population dynamics

Small and large tree seedling community composition differed significantly among the treatments (small seedlings, treatment \times year interaction: $P = 0.002$; large seedlings, treatment \times year interaction: $P = 0.002$). Small and large tree seedling community composition also differed by integrative moisture index classes (small seedlings, $P = 0.002$; large seedlings, $P = 0.004$). Treatment effects were consistent across IMI classes for both the small tree seedling community (treatment \times IMI interaction: $P = 0.15$) and the large tree seedling community (treatment \times IMI interaction: $P = 0.08$). According to successional vector movements in compositional space, post-fire community changes in the small tree seedling community were transient in the burn treatment but thin + burned stands exhibited less resiliency. For example, three growing seasons following treatment application the burn and thin + burn treatments migrated back towards their pre-treatment positions in compositional space; however, recovery along RDA axis 1 occurred at a much slower rate in the thin + burn treatment (Fig. 2a). Large tree seedling community composition remained stable immediately following the treatments. By 2004, successional vectors for all treatments shifted in similar directions (along RDA axis 1) in compositional space (Fig. 2b).

Small-diameter sapling communities differed significantly among the treatments (treatment: $P = 0.002$; treatment \times year interaction: $P = 0.005$) and by IMI class ($P = 0.002$), though treatment effects were consistent across IMI classes (treatment \times IMI interaction: $P = 0.10$). The small-diameter sapling community response mirrored that of the large seedling community. Over time, successional vectors for all treatments

shifted at similar rates and directions in compositional space (Fig. 3a). The large sapling community exhibited no significant treatment \times year interaction ($P = 0.72$), but there was a significant treatment \times IMI interaction ($P = 0.002$) and treatment effect ($P = 0.002$). Compared to prescribed fire, thinning had little effect on large-diameter sapling composition (Fig. 3c).

Changes in community composition among treatments were governed by the population dynamics of dominant tree species. Small seedling densities of the fire-sensitive *A. rubrum* declined immediately following the prescribed surface fires but densities eventually recovered to pre-treatment levels in the thin + burn treatment and exceeded pre-treatment levels in the burn treatment (Fig. 4). In 2004, *A. rubrum* seedling densities in closed-canopy stands (control and burn treatment) were twice as great as thinned stands. In closed-canopy stands (burn treatments and controls) over time, *A. rubrum* achieved greater dominance on xeric and intermediate plots than mesic ones (IMI \times treatment \times year: $F_{6,108} = 2.83$, $P = 0.01$).

L. tulipifera and *S. albidum* dominated the post-fire seedling communities (Fig. 2). Representing only a minor component of the seedling community prior to the treatments (< 2000 stems/ha), *L. tulipifera* increased to $> 70,000$ stems/ha the first-growing season following the surface fires (Fig. 4b). *S. albidum* densities doubled following the surface fires (Fig. 4d), as rootstocks with single stems top-killed by fire tended to sprout multiple stems. In terms of rank order dominance, *S. albidum* remained the second most important species in the seedling stratum across all treatments throughout the study period. *S. albidum* seedling densities were greater on xeric plots than intermediately moist and mesic plots (IMI: $P = 0.009$), a trend consistent among all treatments and years (treatment \times IMI \times year interaction: $P = 0.83$). Seedling densities of the root-suckering *N. sylvatica* also responded positively to surface fires but densities returned to pre-treatment levels over time (Fig. 4c). *N. sylvatica* densities interacted with fire and the moisture gradient (treatment \times IMI: $P = 0.03$); seedling densities in the burn and thin + burn treatment were greater on xeric plots than on intermediate and mesic plots. There were no significant IMI effects or IMI interactions for *L. tulipifera* (all P -values > 0.10).

While the RDA bi-plots indicated that the overstorey dominants in these forests never became an important component of the tree seedling community, canopy-tree seedling densities were dynamic through time (Fig. 5). The first-growing season following prescribed fire, *Carya* seedlings averaged 1000 more stems/ha in the burn and thin + burn treatments than the control and thin treatment (Fig. 5a). However, these differences largely vanished in 2004. *Carya* spp. control densities increased at greater rates than the thin and thin + burn treatment. *Carya* spp. sapling densities initially reduced by fire recovered to control levels by 2004 (Fig. 5a). Seedling densities of *Q. prinus* and *Q. alba* declined over the course of five growing seasons, although only trends in the former species were statistically significant (Fig. 5). Across all sites, *Q. alba* seedling densities declined from 3900 stems/ha in the pre-treatment to 2000 stems/ha in 2004. In contrast, *Q.*

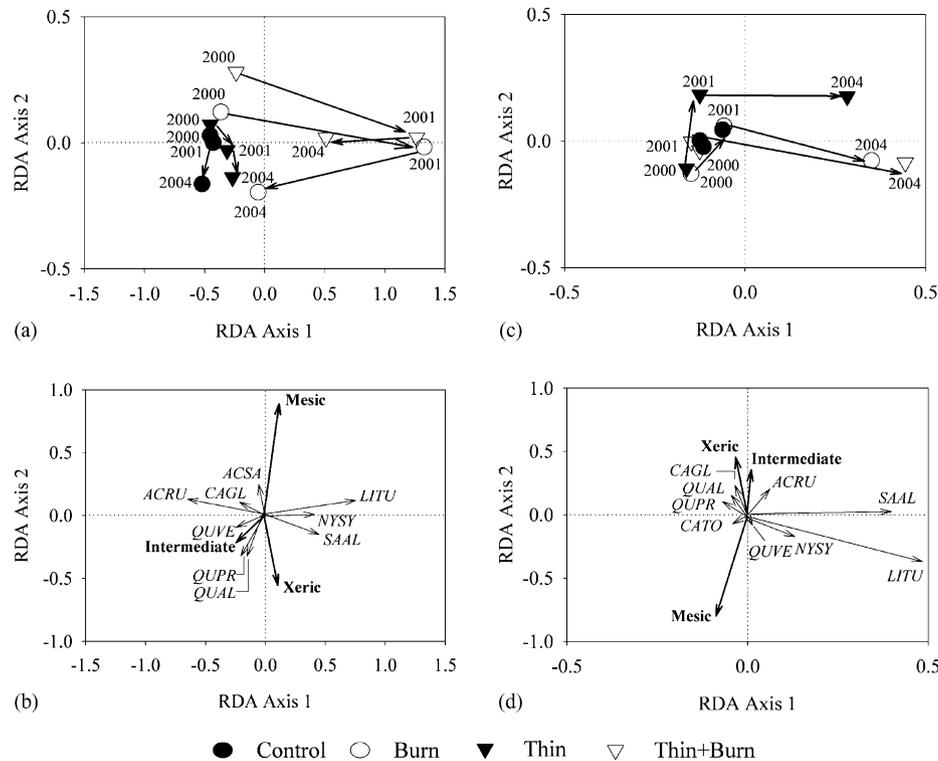


Fig. 2. Redundancy analysis (RDA) ordination plots for the small and large seedling communities in southern Ohio central hardwood forests. Top panels represent treatment ordination. Arrows represent successional vectors depicting the movement of treatments in compositional space over time. Bottom panels represent species ordination with the three integrative moisture index (IMI) classes (xeric, intermediate, and mesic) projected as supplementary 'dummy' variables (ter Braak and Smilauer, 2002). Species abbreviations are as follows: ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; AMAR, *Amalanchier arborea*; CAGL, *Carya glabra*; COFL, *Cornus florida*; FRSP, *Fraxinus* spp.; LITU, *Liriodendron tulipifera*; NYSY, *Nyssa sylvatica*; OXAR, *Oxydendrum arboreum*; QUAL, *Quercus alba*; QUPR, *Quercus prinus*; QUVE, *Quercus velutina*; SAAL, *Sassafras albidum*: (a and b) small seedlings, <50 cm ht; (c and d) large seedlings, 50–140 cm ht.

velutina increased significantly from 2001 to 2004 in the controls and all treatments (Fig. 5d).

A. rubrum remained the numerical dominant of sapling regeneration in all stands (including the controls) four growing seasons following treatment application (Fig. 4). Although a single surface fire initially reduced *A. rubrum* sapling densities, densities recovered to pre-treatment levels by 2004 (Fig. 4a). In contrast, thinning treatments increased densities of *A. rubrum* stems >140 cm ht over time (Fig. 4a). This trend was slightly greater on xeric and intermediate plots relative to mesic ones (treatment \times year \times IMI: $P = 0.05$). *S. albidum* and *L. tulipifera* dominated small-diameter sapling community of the thin + burn treatment in 2004. Sapling densities of *S. albidum* and *L. tulipifera* were <100 stems/ha prior to the treatments but then increased to over 400 stems/ha in the thin + burn treatment (Fig. 4b and d).

Sapling densities for all oak species increased in the thinning treatment but only *Q. alba* exhibited a significant treatment \times year interaction (Fig. 5b–d). Numerically, these increases were minor and saplings of all *Quercus* species remained at exceedingly low densities (<60 stems/ha) the fourth growing following treatment application. While seedling and sapling densities of *Q. alba* and *Q. prinus* did not significantly vary according to IMI class (all P -values > 0.10), *Q. velutina* seedling densities across all treatments were greater on xeric (1770 stems/ha) and intermediately moist plots (1440 stems/

ha) than plots distributed in mesic portions of the watersheds (414 stems/ha) (IMI: $P = 0.006$). IMI \times treatment \times year and IMI \times treatment interactions were non-significant for seedling and sapling densities of all oak species (all P -values > 0.10).

4.3. Tree sprouting

In the 2004 sample, the number of stems originating as sprouts from saplings and canopy trees was significantly different among species and treatments (log-linear analysis: species \times stem origin \times treatment interaction, $P < 0.0001$). Sprouting differences reflected the initial size structure of tree populations prior to the treatments, species sensitivities to prescribed surface fire, and differential growth rates. For example, sprouts from trees >10 cm dbh were largely limited to the dominant mid-story (*A. rubrum*) and overstory species (*Quercus* spp.) in the thinning treatments but were under-represented in other tree species (Fig. 6). While the number of *A. rubrum* sprouts from trees >10 cm dbh was similar among the thinning treatments (Fig. 6), *Q. prinus* and *Q. alba* sprouted at different rates from stumps of felled trees. For *Q. alba*, basal sprouts were greater in the thin treatment compared to the thin + burn treatment, whereas *Q. prinus* exhibited the opposite trend (Fig. 6). The second most abundant sapling species prior to the treatments, *N. sylvatica*, had less stems originating as sprouts from trees <10 cm dbh than *A. rubrum*, the dominant

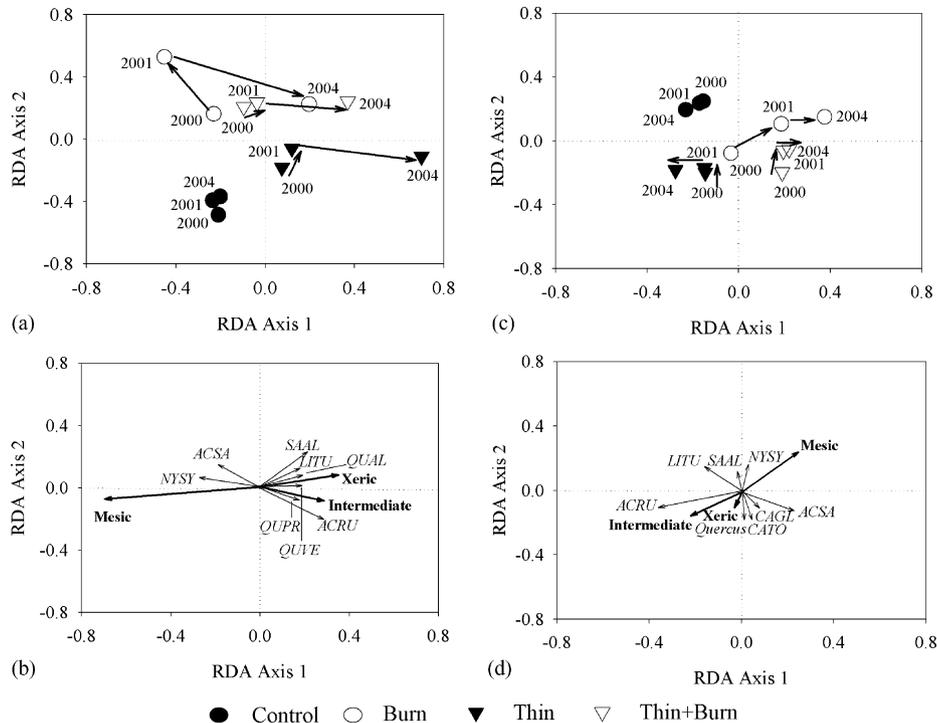


Fig. 3. Redundancy analysis (RDA) ordination plots for the small and large sapling communities in southern Ohio central hardwood forests. Species abbreviations are as follows: ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; AMAR, *Amalanchier arborea*; CACA, *Carpinus caroliniana*; CAGL, *Carya glabra*; CATO, *Carya tomentosa*; COFL, *Cornus florida*; FAGR, *Fagus grandifolia*; FRSP, *Fraxinus* spp.; LITU, *Liriodendron tulipifera*; NYSY, *Nyssa sylvatica*; OXAR, *Oxydendrum arboreum*; QUAL, *Quercus alba*; QUPR, *Quercus prinus*; QUVE, *Quercus velutina*; SAAL, *Sassafras albidum*: (a and b) small saplings, >140 cm ht, <3 cm dbh; (c and d) large saplings, 3–10 cm dbh.

saplings species (Fig. 6). Most *N. sylvatica* stems in the 2004 sample were residual saplings that survived the treatments or represented new cohorts of root-sucker sprouts which initiated following the 2001 fire and grew into the sapling size class (i.e., >140 cm ht). For species that were largely absent from the sapling pool and canopy positions prior to the treatments (i.e., *S. albidum* and *L. tulipifera*), there was little opportunity to resprout from established trees in these forests. Instead, these species recruited into the sapling pool by other means: sprouting from a persistent seedling bank (*S. albidum*) and recruitment from seed (*L. tulipifera*).

5. Discussion

Stand-level restoration treatments applied to 100-year-old central hardwood forest stands changed tree recruitment patterns substantially compared to control stands. Burning treatments initially increased seedling densities and shifted tree regeneration dominance towards shade-intolerant tree species. Whereas early-successional species densities tended to return to pre-treatment levels over time in the burn only treatment, these trends persisted through time in thinned stands. Shifts in dominance to early-successional species beneath silvicultural openings were also reported in managed central hardwood forests of Indiana (Jenkins and Parker, 1998). A single prescribed fire in this study was capable of setting back forest succession to some extent. For example, movement of ordination vectors in the large-seedling and small-diameter

sapling communities in burned stands mirrored that of thinned stands. Small changes in tree community composition following fire parallels prior studies conducted in hardwood forests and reflects the differential capacities of hardwood regeneration to recover following top-kill (Reich et al., 1990; McGee et al., 1995; Kruger and Reich, 1997).

Tree recruitment patterns were largely driven by the initial composition and structure of the stands prior to the treatments, a response generally expected for hardwood forest stands in the understory reinitiation stage of development (Oliver and Larson, 1996). *A. rubrum* maintained dominance in these forests by regenerating from seed, advance regeneration, sapling sprouts, and stumps of felled trees. Arthur et al. (1998) and Swan (1970) also reported a strong resprouting response from established *A. rubrum* regeneration following fire, although reoccurring surface fires are reported to reduce resprouting (Van Lear and Watt, 1993).

Seedling dynamics of the dominant trees in these forests resulted from an interplay between seed availability and anthropogenic disturbances. Prior to the treatments, *A. rubrum* overwhelmed the small seedling communities in these forests, where its small, wind-dispersed seeds readily germinate beneath the thick leaf litter and often carpet the forest floor during non-drought years. A thinning from below treatment as applied in this study reduced the number of seed producing *A. rubrum* trees by approximately one-half (see Table 1). This reduction in potential seed rain probably explains why seedling densities in closed-canopy stands (control and burn treatment)

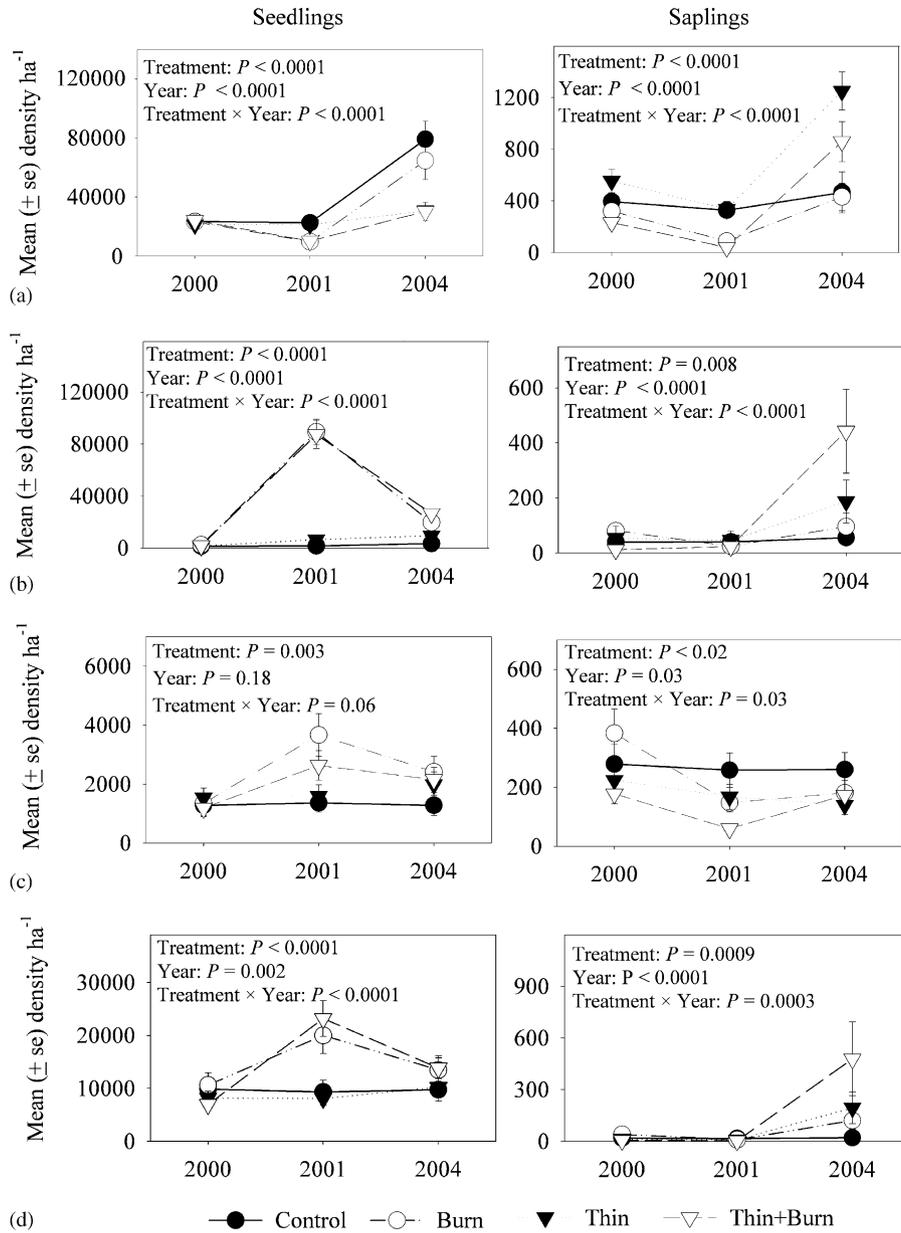


Fig. 4. Temporal trends in tree regeneration densities (mean ± 1 S.E.) for dominant understory species in southern Ohio central hardwood forests. Pre-treatment is represented by 2000, while 2001 and 2004 represent one and four growing seasons following the treatments. Panels on the left-hand column represent seedlings (stems <140 cm tall); panels on the right-hand column represent saplings (stems >140 cm tall but <10 cm dbh). Note differences in scale on y-axis: (a) *Acer rubrum*; (b) *Liriodendron tulipifera*; (c) *Nyssa sylvatica*; (d) *Sassafras albidum*.

were twice as great as those in thinned stands in 2004. In these forests, *A. rubrum* seedling densities declined only in years immediately following fire (Hutchinson et al., 2005a); recently established seedlings are poor resprouters following top-kill since root collar buds are often positioned at the soil surface and therefore poorly protected from the intense heat experienced during ground fires (Huddle and Pallardy, 1996; Brose and Van Lear, 2004). *A. rubrum* rapidly recolonized the seedling community of burned stands due to the presence of seed producing trees in the mid-story and sub-canopy positions, which are largely unaffected by these prescribed surface fires. Small seedling community changes immediately following fire

were largely driven by *L. tulipifera* swapping rank order of dominance with *A. rubrum*. *L. tulipifera* was uncommon in the understory at the study onset probably because the single-tree fall gap disturbances in these forests provided little recruitment opportunities (Busing, 1995), although it probably maintains a persistent seed bank in these forests due the presence of a small number of canopy trees (Beck, 1965; Sander and Graney, 1992). Leaf litter acts as a physical barrier to *L. tulipifera* seed germination, thus the consumption of consolidated leaf litter on the forest floor during fire can facilitate colonization from buried seed (Shearin et al., 1972). However, repeated fires may eventually exhaust its forest floor seed bank and eliminate new

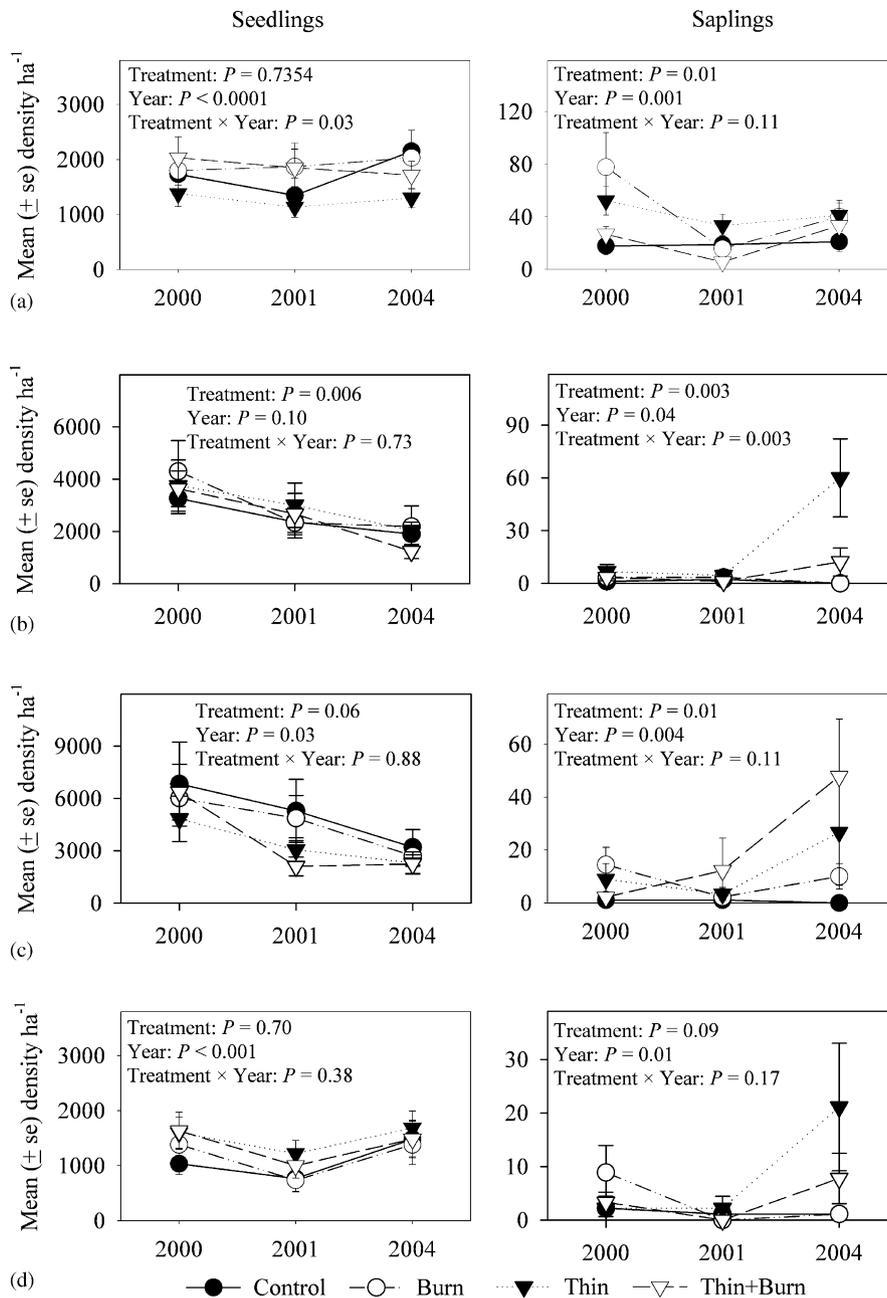


Fig. 5. Temporal trends in tree regeneration densities (mean \pm S.E.) for oak and hickory, the dominant overstory components of southern Ohio central hardwood forests. Pre-treatment is represented by 2000, while 2001 and 2004 represent one and four growing seasons following the treatments. Panels on the left-hand column represent seedlings (stems <140 cm tall); panels on the right-hand column represent saplings (stems >140 cm tall but <10 cm dbh). Note differences in scale on y-axis: (a) *Carya* spp.; (b) *Quercus alba*; (c) *Quercus prinus*; (d) *Quercus velutina*.

recruits which are considered intolerant of fire (Beck, 1965; Brose, 1999).

While we did not directly measure seed rain in this study, several lines of evidence suggest that oak seedling dynamics may, in part, have been controlled by differential seed production. A bumper acorn crop resulted in a large cohort of oak seedlings establishing in adjacent forests in 1996 (Hutchinson et al., 2005a), although no considerable acorn crops occurred thereafter (Riccardi et al., 2004). Seedling densities of *Q. alba* and *Q. prinus* reflected irregular acorn

production; densities were greatest at the study onset but then incrementally declined in all treatments over the 5-year study period, suggesting that seedling mortality exceeded establishment. This demographic trend follows the 'population wave' pattern described by Johnson et al. (2002), whereby periodic masting events are associated with pulses of recruitment followed by natural thinning of the cohort over time. Low-light levels may have also contributed to seedling declines, even in thinned stands where only modest increases (7% over control and burn stands) in light levels were reported (Iverson et al.,

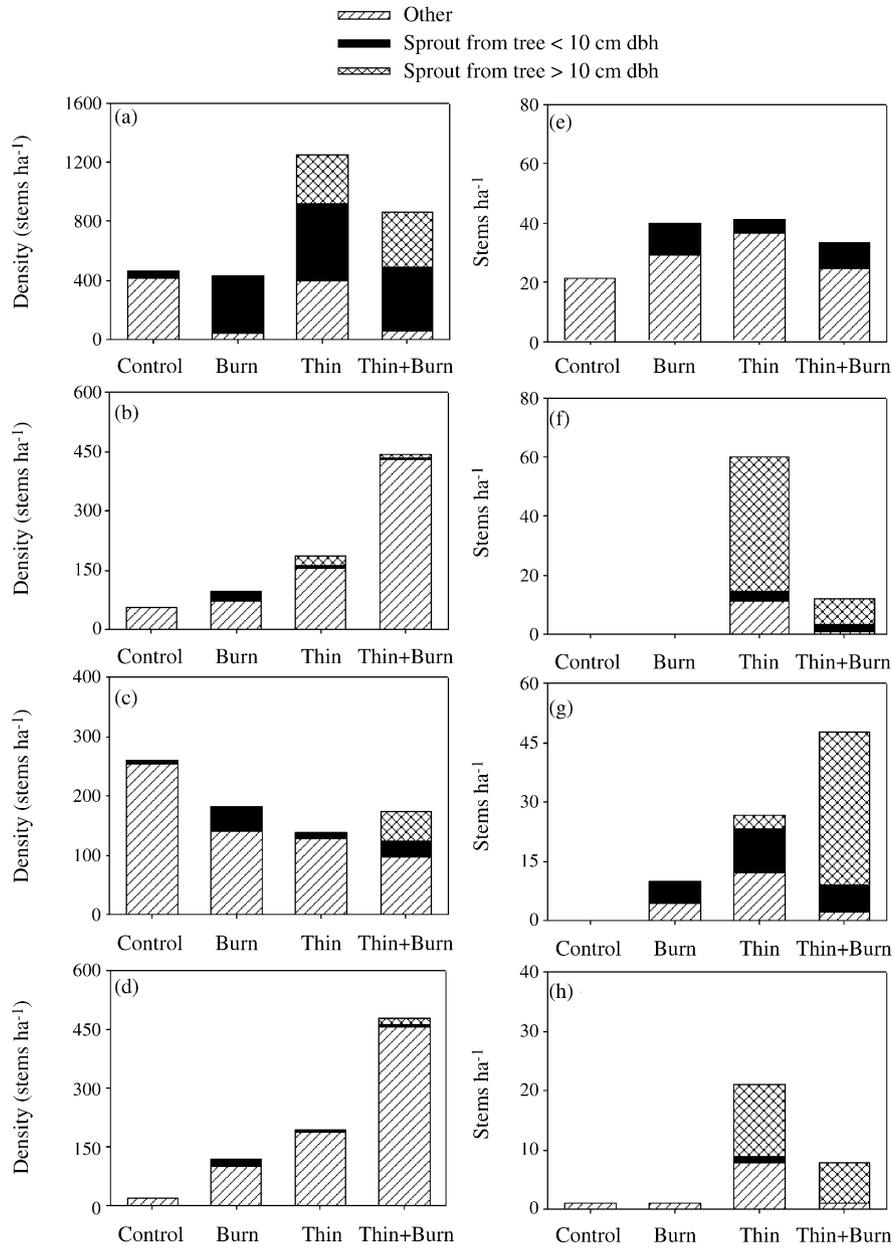


Fig. 6. Distribution of stems >140 cm in height among treatments in 2004. Stems that were classified as 'other' includes residual stems that survived the treatment, and stems that recruited into the sapling stratum by seed or seedling sprout. Left-hand panel represents understory dominants and right-hand panel represents overstory dominants. Note differences in scale on y-axis: (a) *Acer rubrum*; (b) *Liriodendron tulipifera*; (c) *Nyssa sylvatica*; (d) *Sassafras albidum*; (e) *Carya* spp.; (f) *Quercus alba*; (g) *Quercus prinus*; (h) *Quercus velutina*.

2004a). Over a 5-year period, Crow (1992) reported that 92% of artificially planted oak seedlings survived in open habitats whereas only 54% and 36% survived in partially closed and completely closed forests, respectively. In contrast, *Q. velutina* seedling densities increased in all treatments over time, suggesting that seed availability was not as limiting, or perhaps environmental conditions were more suitable for establishment. Seed trap studies conducted from 2000 to 2001 at two of the sites (REMA and Zaleski) reported that seed-producing *Q. velutina* trees produced three times more viable acorns than *Q. prinus* (Riccardi et al., 2004). As seed availability increases, predators are more likely to become satiated, thus providing

more opportunities for recruitment from seed. This can offset seedling mortality in pre-existing cohorts and stabilize regeneration densities (Johnson et al., 2002).

Temporal variability in the population dynamics of oak seedlings occurred independent of any treatment effects. We detected no treatment × year interactions for seedling densities of the dominant oaks (*Q. alba*, *Q. prinus*, and *Q. velutina*). While stems >140 cm in height increased in thinned stands for all the dominant oaks, a large proportion of these stems originated as stump sprout reproduction from felled trees >10 cm dbh, rather than seedling sprouts released from growth suppression. Although stump sprouts exhibit faster growth rates

than seedling sprouts, they cannot alone sustain oak overstory replacement in mature second-growth stands (Sander and Graney, 1992; Dey, 2002). Moreover, our sampling scheme enumerated all stems arising from a single stump. Assuming only a single stump sprout can achieve canopy dominance (Oliver and Larson, 1996), the potential for overstory replacement is probably much lower than the absolute densities we report here.

Results presented here parallel other prescribed fire studies in closed-canopy oak systems of Kentucky (Arthur et al., 1998; Kuddes-Fischer and Arthur, 2002) and forests where fire occurred immediately before or following silvicultural thinning treatments (Johnson, 1974; Wendel and Smith, 1986; Van Lear and Waldrop, 1989; McGee et al., 1995; Franklin et al., 2003). Although in other oak-dominated systems oak regeneration responded positively to a surface fire at short-time scales, these studies occurred in forest stands that were silviculturally thinned several years prior to burning (Kruger and Reich, 1997; Brose and Van Lear, 1998). Collectively, these results support the supposition that the timing of prescribed fire following a thinning treatment may be critical for promoting oak recruitment. Applying fire several years after canopy removal allows oak seedlings to allocate carbohydrate reserves to belowground tissue, thus facilitating the development of large root systems. As below- to aboveground biomass increases, oak seedlings exhibit a greater probability of resprouting into larger size classes following top-kill by fire thereby improving their competitive rank with fast-growing, opportunistic tree species (Larsen and Johnson, 1998; Brose et al., 1999). Since fire was applied in this study the spring immediately following a dormant season thinning treatment, there was no time for suppressed oak seedling populations to physiologically respond to increased solar radiation levels in thinned stands.

In general, silvicultural thinning treatments are expected to improve oak recruitment only if understory and midstory competitors are suppressed (Loftis, 1990; Brose et al., 1999). Increased light levels associated with thinned stands stimulated rapid ingrowth of early-successional species into the small sapling stratum, and increased shrub cover of early-successional species. Collective stem densities of large seedlings and small-diameter saplings in thinned and thinned + burned stands were two times greater than those recorded at the study onset. Moreover, RDA bi-plots indicated that oak regeneration was primarily distributed in xeric and intermediate plots, where recruitment of its dominant understory competitors was accelerated. By 2004, *A. rubrum*, *L. tulipifera*, and *S. albidum* regeneration (stems <10 cm dbh) outnumbered oak regeneration by at least a factor of two in each treatment. This rapid ingrowth and recruitment could mediate light resources beneath canopy openings, thereby offsetting the intended benefits of a silvicultural thinning treatment. In an Appalachian mixed-oak forest, for example, Chiang et al. (2005) found that hardwood sprouts (primarily *A. rubrum*) stimulated by reoccurring surface fires overtopped oak regeneration beneath canopy breaks, resulting in light conditions similar to unburned plots. *L. tulipifera* was favored over oak regeneration in group selection

cuts in mature Indiana central hardwood forests (Jenkins and Parker, 1998), while Ehrenfeld (1980) found that *A. rubrum* dominated large canopy openings in mature New Jersey oak forests where oak seedling were present in the understory.

Prescribed fires applied in thinned and closed-canopy stands resulted in sustained reductions in large-diameter (3–10 cm dbh) sapling densities over the 4-year period. Our results differ somewhat with those reported after a low intensity surface fire in Kentucky upland central hardwood oak forests, where Franklin et al. (2003) reported significant declines in saplings <3.8 cm dbh but was unable to detect significant declines in stems >3.8 cm dbh. In southern Appalachian mixed-oak forests, Elliot et al. (1999) found that fire interacted with the topographic gradient: high intensity fires on dry ridgetops resulted in significant declines of *A. rubrum* and *N. sylvatica* stems >5 cm dbh, whereas sapling declines were not observed on mesic, lower slope positions where fires burned at a much lower intensity (Elliot et al., 1999). Likewise, we found sapling densities in mesic plots were reduced at lower rates than on xeric and intermediate plots. A significant IMI × treatment interaction in the large sapling stratum in our community-level analysis suggests that lower slope, mesophytic trees (mainly *A. saccharum*) tended to survive the surface fires at greater densities than saplings distributed in upslope positions (primarily *A. rubrum* and *N. sylvatica*). This pattern likely resulted from differential fire intensities across the topographic moisture gradient; on average, dormant season fires in moist, sheltered sites burned at lower intensities than in drier, upper slope positions (Iverson et al., 2004b). In topographically complex oak systems in the Missouri Ozarks, Blake and Schuette (2000) similarly reported greater persistence of *A. saccharum* in mesic portions of burned stands. This also supports previous findings in long-unburned forests that large shade-tolerant tree regeneration can develop bark thick enough to survive a single surface fire (Harmon, 1984).

6. Conclusions and management implications

Prescribed burning and silvicultural thinning treatments are potential options for managing succession in central hardwood oak forests. Short-term management objectives should include increasing understory light levels to stimulate oak regeneration, reducing the dense horizontal and vertical structure that has resulted from decades of recruitment by shade-tolerant species, and preventing what seemingly appears to be forest dominance by *A. rubrum*. These treatments are guided by historical data that suggest periodic surface fires and canopy disturbances played a key role in the development and stability of central hardwood oak forests. In the absence of larger-scale disturbances, oak forests may be a transitional community in which gap replacement processes favor shade-tolerant species over oak.

As part of a long-term ecosystem management project, the results presented here represent only the initial response (4 years) of tree regeneration to experimental anthropogenic disturbances. Our data agree with the conclusions of previous studies that a single prescribed surface fire in a mature oak

forest provides few opportunities for oak regeneration, largely because one fire is unable to reduce competitor densities and create large enough canopy openings needed for oak recruitment. While repeated fires are planned for these singly burned stands, it is not yet clear if conducting repeated fires beneath intact canopies is a suitable management prescription. At sites adjacent to ours, stands receiving annual and periodic fires during the dormant season resulted in little oak recruitment over a 6-year period, although herb-layer diversity increased and stands began to resemble the more open-structured forests described at the time of Euro-American settlement (Hutchinson et al., 2005a,b). In forests where management objectives call for rapid oak recruitment, managers may need to use mechanical thinning to reduce a midstory and overstory densities that seems to suppress oak recruitment.

One problem with using mechanical thinning treatments in mature central hardwood stands is the dense seedling and sapling bank that is often present during the later stages of stand understory reinitiation. Silvicultural prescriptions that call for moderate canopy thinning treatments without a follow-up program of prescribed fire result in stands with a dense understory of unwanted, fast-growing tree regeneration that can overtop oak seedling sprouts. Tree-ring data indicate that mechanical thinning treatments which partially removes an oak overstory can accelerate the recruitment of suppressed shade-tolerant trees in the understory, resulting in stands that virtually exclude oak as a dominant or co-dominant component (Abrams and Nowacki, 1992; Tift and Fajvan, 1999).

Prescriptions that follow a canopy thinning treatment with an understory treatment (e.g., prescribed fire or herbicide) may

delay or suppress such a pathway altogether (Loftis, 1990; Brose et al., 1999). However, the timing and execution of understory treatments are likely to be critical. Our data indicate that applying fire immediately following a thinning treatment promotes early-successional regeneration, accelerates sprouting of oak competitors and seems to provide little benefit, at least in this short-term, for oak regeneration. Periodic fires should be reapplied to reduce resprouting and early-successional recruitment (Van Lear and Watt, 1993). Future studies in central hardwood forests should explore the effects of varying the timing, intensity, and seasonal application of fire in conjunction with a mechanical thinning treatment. At sites where tree harvest is restricted or impractical, managers may need to conduct an occasional high-severity fire or growing season fire to reduce resprouting rates.

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Appendix A. Seedling (<140 cm tall) stems/ha for common tree species among forest management treatments

	Control			Burn			Thin			Thin + burn		
	2000	2001	2004	2000	2001	2004	2000	2001	2004	2000	2001	2004
<i>Acer rubrum</i>	45067	38117	89867	41467	14133	75600	42883	40150	42467	43667	14350	35350
<i>Acer saccharum</i>	133	433	917	167	367	9917	283	517	2033	167	833	950
<i>Amalanchier arborea</i>	1250	1333	1383	467	517	350	1483	1133	1083	783	483	667
<i>Carpinus caroliniana</i>	500	867	800	167	33	150	233	267	700	750	467	567
<i>Carya cordiformis</i>	233	300	167	33	433	83	183	83	17	367	683	250
<i>Carya glabra</i>	850	1117	1467	767	883	1050	650	833	883	533	567	833
<i>Carya tomentosa</i>	650	283	517	967	500	833	533	200	400	1133	500	617
<i>Cercis canadensis</i>	83	17	67	17	50	67	50	0	117	183	300	350
<i>Cornus florida</i>	700	317	483	400	300	183	500	1083	483	283	150	250
<i>Fagus grandifolia</i>	433	450	300	17	0	50	217	200	283	67	0	183
<i>Fraxinus</i> spp.	650	767	583	250	267	117	900	767	833	2183	1650	1850
<i>Liriodendron tulipifera</i>	1283	1533	3317	2267	89300	19583	1250	6417	9350	1733	87267	26417
<i>Nyssa sylvatica</i>	1283	1333	1283	1350	3667	2417	1533	1600	1983	1183	2633	2150
<i>Oxydendrum arboreum</i>	1333	1167	633	1533	2783	1883	583	1100	1783	233	617	4383
<i>Populus grandidentata</i>	0	0	0	0	67	50	33	150	83	0	317	183
<i>Prunus serotina</i>	533	617	683	367	550	350	617	450	367	1483	650	467
<i>Quercus alba</i>	3267	2367	1900	4300	2333	2167	3583	3000	2033	3633	2667	1233
<i>Quercus coccinea</i>	1083	550	1183	2433	2050	1817	2033	1733	1817	1050	883	1483
<i>Quercus prinus</i>	6833	5283	3200	6017	4767	2700	4833	3050	2300	6367	2100	2233
<i>Quercus rubra</i>	383	1000	250	633	850	567	450	867	417	583	1617	400
<i>Quercus velutina</i>	1033	1033	1483	1383	733	1383	1600	1217	1683	1633	1000	1483
<i>Sassafras albidum</i>	9850	9333	9733	10617	19983	13367	8133	8067	10217	6933	23183	13833
<i>Ulmus rubra</i>	750	833	550	2000	1733	1267	983	867	1517	4200	2617	4167

Appendix B. Sapling (>140 cm ht < 10 cm dbh) stems/ha for common tree species among forest management treatments

	Control			Burn			Thin			Thin + burn		
	2000	2001	2004	2000	2001	2004	2000	2001	2004	2000	2001	2004
<i>Acer rubrum</i>	394	327	466	320	88	430	553	420	1250	232	238	859
<i>Acer saccharum</i>	30	33	43	182	109	71	189	127	103	224	74	77
<i>Amalanchier arborea</i>	2	2	2	7	4	4	19	16	26	20	0	2
<i>Carpinus caroliniana</i>	18	18	22	11	0	0	12	6	52	52	10	23
<i>Castanea dentata</i>	3	2	2	10	6	14	0	1	9	2	0	6
<i>Carya glabra</i>	7	10	6	34	10	18	32	13	22	14	3	17
<i>Carya tomentosa</i>	11	9	16	42	4	22	20	19	18	11	2	14
<i>Cercis canadensis</i>	7	4	6	1	0	1	3	7	6	7	1	7
<i>Cornus florida</i>	26	27	14	19	6	4	43	23	23	49	8	18
<i>Fagus grandifolia</i>	319	309	316	62	17	10	98	52	78	37	14	6
<i>Fraxinus</i> spp.	20	22	19	23	7	1	58	41	89	33	6	54
<i>Liriodendron tulipifera</i>	39	40	56	80	24	96	53	46	187	11	23	442
<i>Nyssa sylvatica</i>	279	258	260	383	148	181	223	168	139	178	63	173
<i>Oxydendrum arboreum</i>	87	96	141	164	50	216	84	63	209	50	20	169
<i>Quercus alba</i>	1	2	0	3	3	0	6	4	60	3	1	12
<i>Quercus coccinea</i>	0	0	0	0	0	0	3	1	26	0	0	14
<i>Quercus prinus</i>	1	1	0	14	2	10	9	3	27	2	12	48
<i>Quercus rubra</i>	4	0	0	12	1	3	4	2	19	4	1	10
<i>Quercus velutina</i>	2	1	1	9	0	1	2	2	21	3	0	8
<i>Sassafras albidum</i>	19	16	20	40	9	120	12	8	194	4	2	479
<i>Tilia americana</i>	1	1	0	1	0	0	8	6	2	23	3	19
<i>Ulmus rubra</i>	7	0	0	9	2	1	0	2	0	2	0	0

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