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Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio

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Abstract

This study quantifies prescribed fire effects at four sites in southern Ohio, from 1995 to 2002. Each site had three treatment units: an unburned control, a unit burned 2× (1996 and 1999), and a unit burned 4× (1996–1999). Vegetation plots were stratified by an integrated moisture index (IMI) into xeric, intermediate, and mesic classes. Prior to treatments, oak (*Quercus* spp.) and hickory (*Carya* spp.) comprised 74–83% of basal area among sites but shade-tolerant species (e.g., *Acer rubrum*) were abundant in the midstory and completely dominated the sapling layer. Fires were conducted in March and April. Fire intensity, estimated by temperature-sensitive paints, was highest on the 2× burn units. Fires had little effect on large tree (>25 cm DBH) density and stand basal area. By contrast, the density of small trees (10–25 cm DBH) was reduced by 31% on 2× burn units and by 19% on 4× burn units. "Fire-induced" mortality (i.e., mortality on burn units above that of unburned units) for the most common species of small trees was: *A. rubrum* = 33%; *Quercus alba* = 17%; *Carya* spp. = 13%; *Nyssa sylvatica* = 10%; *Acer saccharum* = 4%; *Quercus prinus* = 2%. Sapling density was reduced by 86% on burn treatments. Despite reduced small tree and sapling densities on burned units, canopy openness, estimated by hemispherical photography, remained low (<6%). In general, the composition of tree regeneration was not substantially altered by fire treatments. On burn units, a significant initial decrease in *A. rubrum* seedling density and a significant increase in *Liriodendron tulipifera* from the seed bank did not persist throughout the study. Oak + hickory seedling density was not significantly affected by fire nor was the density of shade-tolerant seedlings. Post-treatment (2002) sampling of large seedlings (>30 cm height) indicated no significant differences in the abundance of oak + hickory nor that of shade-tolerant seedlings among fire treatments. For most vegetation response variables, fire effects tended to be similar among IMI classes. The application of fire alone, without partial harvesting, failed to improve oak regeneration consistently. However, given that two fires reduced stand density, the longer term application of periodic fire, coupled with natural gap dynamics, may still be a feasible management strategy for improving the sustainability of oak forests where harvesting is not permitted or desired.

Keywords: *Quercus*; *Acer*; Oak–hickory forest; Fire; Prescribed burning; Sustainability; Mortality; Central hardwoods region

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1. Introduction

Forests, woodlands, and savannas dominated by oak occupied much of the eastern United States prior to Euro-American settlement (Nuzzo, 1986; Delcourt and Delcourt, 1987; Whitney, 1994; Abrams, 2002). Evidence from fossil charcoal and pollen (Clark and Royall, 1995; Foster et al., 2002), fire-scarred trees (Cutter and Guyette, 1994; Shumway et al., 2001; Guyette et al., 2003), and early land surveys (Batek et al., 1999) suggest that fire was frequent in oak-dominated landscapes, and presumably promoted oak over more fire-sensitive species. Written accounts indicate that Native Americans used fire frequently for a variety of purposes (Day, 1953; Whitney, 1994) and anthropogenic fire continued in many areas after Euro-American settlement until fire suppression policies were adopted, ca. 1920 (Sutherland, 1997; Shumway et al., 2001; Schuler and McClain, 2003).

Today oak–hickory remains the most abundant forest type in the United States (Smith et al., 2001); many older stands (>80 years) are dominated by oak regenerated following exploitive timber harvesting (ca. 1850–1900) but prior to fire suppression. Numerous studies indicate that oak is decreasing in abundance in most areas and is being replaced by more mesic- and fire-sensitive species (e.g., Lorimer, 1984; Abrams, 1992). In most landscapes, oak advance regeneration (large seedlings and saplings) is sparse and also declines markedly from xeric poor-quality sites to mesic high-quality sites (Johnson et al., 2002). Fire suppression is widely considered a primary cause of declining oak dominance (Abrams, 1992; Lorimer, 1993). In forests where large populations of non-oak species have established in the midstory and understory layers, timber harvesting can accelerate the replacement of oak (Abrams and Nowacki, 1992; Schuler, 2004).

The "hill country" of southeastern Ohio is characterized by highly dissected topography which creates strong local-scale (e.g., watershed-scale) gradients in vegetation and soils (Morris and Boerner, 1998; Hutchinson et al., 1999). Mixed-oak forests dominated the region just prior to Euro-American settlement, ca. 1800 (Gordon, 1969; Dyer, 2001). Though the oak–hickory forest type remains abundant (Griffith et al., 1993), shade-tolerant species, such as red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and blackgum (*Nyssa sylvatica*), now dominate the midstory and understory of most mature oak forests (Goebel and Hix, 1996; McCarthy et al., 2001; Hutchinson et al., 2003a). Fire-scarred trees indicate that fires were frequent from ca.1880 to 1930, when many forests were regenerating after land clearance (Sutherland, 1997; Sutherland et al., unpublished data). Fire suppression was instituted in 1923, sharply reducing the acreage burned (Leete, 1938; Sutherland et al., 2003).

Prescribed fire has been recommended to improve the sustainability of oak forests (Van Lear and Watt, 1993; Lorimer, 1993; Johnson et al., 2002; McShea and Healy, 2002). Fire might improve the regeneration potential of oak by: (1) reducing tree density and canopy cover thus increasing light levels on the forest floor, (2) reducing competition from more fire-sensitive saplings and seedlings in the understory, and (3) creating seedbed conditions more favorable to oak establishment. Studies have shown that fire alone (Barnes and Van Lear, 1998; Adams and Rieske, 2001), fire surrogates (Lorimer et al., 1994), or fire coupled with partial canopy removal (Kruger and Reich, 1997; Brose and Van Lear, 1998; but see Wendel and Smith, 1986) can improve the competitive status of oak seedlings. However, results from a number of studies have been inconclusive (e.g., Arthur et al., 1998; Elliott et al., 1999; Franklin et al., 2003; Gilbert et al., 2003). These variable responses are understandable given different forests (composition, site quality, and land-use history), fire behavior and seasonality, and the periodic nature of oak reproduction (mast production). All of those studies were relatively short-term in duration and some were conducted at relatively small scales and/or lacked replication at multiple sites.

In 1995, we initiated a study of prescribed fire effects on the composition, structure and regeneration of mixed-oak forests. This study is a component of a larger multidisciplinary project examining fire effects in oak forest ecosystems (Sutherland et al., 2003). The study is located at four sites in southern Ohio, each with three long-term fire frequency treatments: unburned, frequent fire, and infrequent fire. Study plots were stratified by a GIS-derived integrated moisture index (IMI) into three classes: xeric, intermediate, and mesic. Our primary objectives were to: (1) determine the extent to which fire can alter stand structure and composition, (2) determine whether fire can improve the competitive status of oak + hickory regeneration relative to maples and other species, (3) compare the effects of two different fire frequencies on forest structure and regeneration, and (4) compare fire intensity and effects across the topographic moisture gradient. Here, we analyze fire effects over an 8-year period (1995–2002), during which the frequent units were burned annually 1996–1999 (burned 4×) and the infrequent units were burned in 1996 and 1999 (burned 2×).

2. Methods

2.1. Study areas

The study area is in the southern unglaciated Allegheny Plateau Region of southeastern Ohio with topography that is highly dissected, characterized by high hills, sharp ridges, and narrow valleys (McNab and Avers, 1994). Parent materials are primarily sandstones and shales of Pennsylvanian origin (Boerner and Sutherland, 2003). Soils are mostly silt loams that are acidic and well drained (Boerner et al., 2003). Mean annual temperature, precipitation, and frost-free days are 11.3 °C, 1024 mm, and 158 days, respectively (Sutherland et al., 2003). The region has two distinct fire seasons in which nearly all fires occur: early-spring (March–April) and fall (October–November) (Sutherland et al., 2003).

Four study sites were selected in 1994, each composed of >75 ha of mixed-oak forest >80 years since clearcutting. Arch Rock (AR) (39°11′N, 82°22′W) and Watch Rock (WR) (39°12′N, 82°23′W) are located in Vinton County within the Vinton Furnace Experimental Forest (VFEF). The VFEF is owned by Escanaba Timber LLC (formerly MeadWestvaco Corporation) and co-managed by the USDA Forest Service, Northeastern Research Station. Young's Branch (YB) (38°43′N, 82°41′W) and Bluegrass Ridge (BR) (38°36′N, 82°31′W) are located in Lawrence County on the USDA Forest Service's Wayne National Forest, Ironton Ranger District.

Early land surveys (ca. 1800) indicate that oaks and hickories comprised 56–79% of witness trees in the townships encompassing the study sites and white oak (*Quercus alba*) was the most abundant species (Hutchinson et al., 2003b). Maples and beech comprised only 8–22% of witness trees, and were recorded primarily in ravines and stream valleys. Pine (*Pinus* spp.) and American chestnut (*Castanea dentata*) also were infrequent. Euro-American settlement began in the early 1800s and the upland forests of all four sites were presumably clearcut for the charcoal iron industry in the mid- to late-1800s (Hutchinson et al., 2003b). Since that time, forests have undergone secondary succession. Stand-level canopy disturbances, determined by release events in tree cores, have occurred at all sites, likely the result of both selective harvesting and natural factors, e.g., drought (Hutchinson et al., 2003b). Fires occurred frequently in the region until suppression began in 1923 (Leete, 1938; Sutherland, 1997; Sutherland et al., 2003). White-tailed deer density for Vinton County is estimated to be 6.3 km^{-2}; browsing does not appear to be a major limiting factor to tree regeneration (Apsley and McCarthy, 2004).

Forests on the four sites were generally similar in age, structure, and composition prior to treatments (Table 1). Among sites, average tree basal area and tree density ranged from 25 to 28 m^2/ha and 354–416 trees/ha, respectively. Oaks and hickories dominated the larger size classes of trees (>25 cm DBH) and comprised 74–83% of basal area (Table 1, Fig. 1). Among the oaks and hickories, *Q. alba* was most abundant, followed by *Quercus prinus*, *Carya* spp., and *Q. velutina* (Yaussy et al., 2003). Shade-tolerant species, including *A. rubrum*, *A. saccharum*, and *N. sylvatica* dominated the sapling layer (1.4 m height to 9.9 cm DBH) and the 10–15 cm DBH size class (Fig. 1). Among sites, oak and hickory species comprised 48–64% of trees, 7–19% of seedlings, and only 1–9% of saplings.

2.2. Experimental design

Each site included three long-term fire treatment units (~25 ha each): a control (unburned), infrequent burn, and frequent burn. From 1996 to 1999, the frequent burn units (hereafter "burned 4×") were burned annually and the infrequent burn units (hereafter "burned 2×") were burned in 1996 and 1999.

To account for variation in soil moisture and vegetation across the landscape, a GIS-derived

Table 1
Study site attributes (means ± 1 S.E.) in 1995 prior to prescribed fire treatments

Attribute	Study site			
	Watch Rock	Arch Rock	Young's Branch	Bluegrass
Area (ha)	76.8	80.1	75.3	109.3
Stand age (years)	112 + 4.6	108 ± 2.1	121 ± 5.3	100 ± 3.9
Tree basal area (m^2/ha)	25.3 ± 0.7	27.2 ± 0.7	27.8 ± 0.8	27.1 ± 0.9
Tree density (trees/ha)	369 ± 14.4	375 ± 11.0	416 ± 22.7	354 ± 8.5
Sapling density (saplings/ha)	1922 ± 137	2101 ± 185	2385 ± 151	2628 ± 277
Tree seedling density (ha)	24028 ± 4157	25602 ± 2992	32176 ± 3562	51806 ± 7438
Oak + hickory basal area (%)	75.9 ± 4.1	83.4 ± 2.9	73.9 ± 3.8	78.2 ± 4.7
Oak + hickory trees/ha (%)	55.1 ± 4.4	63.9 ± 3.9	47.5 ± 3.2	61.1 ± 5.1
Oak + hickory saplings/ha (%)	9.2 ± 3.3	7.0 ± 2.9	1.2 ± 0.4	2.7 ± 0.7
Oak + hickory seedlings/ha (%)	14.1 ± 2.3	19.4 + 3.4	10.2 ± 2.3	7.3 ± 1.5

Data were collected on $n = 27$ plots per study site.

integrated moisture index was used to stratify the landscape by long-term moisture status (Iverson et al., 1997). The components of the IMI were a slope-aspect shading index (40%), the cumulative flow of water downslope (30%), soil water-holding capacity (20%), and curvature of the landscape (10%). An IMI score was calculated for each 30 m × 30 m pixel and each pixel was then classified as xeric, intermediate, or mesic. A description of the IMI and its application to this study are provided in Iverson et al. (1997) and Iverson and Prasad (2003).

Within each treatment unit, nine 50 m × 25 m (0.125 ha) vegetation plots were established, for a total of 108 plots (Sutherland et al., 2003). We intended to place three plots in each of the three IMI classes per treatment unit. However, after establishment plots were geo-referenced and approximately 20% had not been located in the intended IMI class, resulting in an uneven distribution of vegetation plots by IMI class among treatment units. Only three of the twelve treatment units contained fewer than two or more than five plots in a single IMI class; AR unburned had only one intermediate plot, BR 4× had only one mesic plot, and BR unburned was the most unbalanced unit, containing one xeric plot, seven intermediate plots, and one mesic plot. The experimental design is a split-plot, with fire as the whole-plot effect and IMI as the split-plot effect; the 0.125-ha vegetation sampling plots were designed as pseudoreplicates within each IMI class.

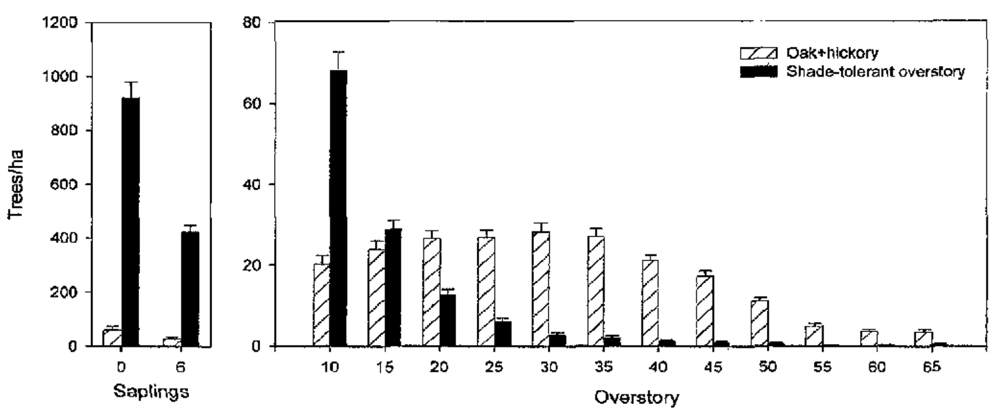

Fig. 1. Mean (±1 S.E.) pre-treatment tree density across all 108 plots, for oak + hickory and shade-tolerant overstory species. Each pair of bars represents the DBH size class (e.g., 10 = 10–14.9 cm DBH). The 0 sapling size class includes all stems >1.4 m height to 5.9 cm DBH.

2.3. Prescribed fires

Prescribed fires ($n = 24$ total, 1996–1999) were conducted from March 21 to April 21, before trees were in leaf and before most understory vegetation had emerged. Only four fires, all in 1996, occurred after April 15. Maximum air temperatures on burn days averaged 22 °C (72 °F) and ranged from 10 to 31 °C (50–88 °F). Relative humidities ranged from 20 to 45% during the fires. From 1996 to 1998, all burns occurred 1–6 days after a measurable ($\geq$1 mm) precipitation event. In 1999, all eight burns occurred $\geq$12 days after measurable precipitation, though maximum air temperatures were cool, ranging from 10 to 19 °C (50–66 °F). Most of the landscape was burned with strip-headfires. Flame lengths were usually <1 m; flame lengths of 1–2 m were much less common and flame lengths >2 m were only seldom observed. On average, 86% of the landscape burned per fire, based on estimates for each vegetation plot (Hutchinson, 2004). Fuel consumption was limited primarily to unconsolidated leaf litter and small woody debris (1-h fuels) (Hutchinson, personal observation).

As a surrogate measure of fire intensity during the fires, we recorded the melting points of temperature-sensitive paints. We applied Tempilac® (Tempil Corporation, New York) paints to aluminum tree tags; the six paints were engineered to melt at 79, 121, 163, 204, 316, and 427 °C. On each plot, we placed a painted tag 25 cm above the ground at the four corners and at the midpoint along each of the two 50 m plot axes. After the fires, we inspected the tags and the mean of the six tags per plot was used for subsequent data analysis.

2.4. Sampling and measurements

2.4.1. Vegetation

All overstory trees ($\geq$10 cm DBH) were tallied by species in each plot in 1995 (pre-treatment), 1997, 1999, and 2002. Each tree was permanently marked and we recorded its mortal status and DBH each sample year. Tree saplings (1.4 m height to 9.9 cm DBH) were tallied in one-quarter of each plot (312.5 m^2 subplot) each year 1995–1999 and in 2002. The sapling subplot was a right triangle (25 m × 25 m × 35.4 m), with the hypotenuse running from upslope midpoint of the plot to an opposing downslope corner. Saplings were recorded in three size classes: 1.4 m height to 2.9 cm DBH, 3.0–5.9 cm DBH, and 6.0–9.9 cm DBH. Most saplings resprouted after topkill but were tallied on the sapling plots only if $\geq$1.4 m height, which was very uncommon throughout the study. Sprouts from trees and saplings that were <1.4 m height were only tallied if present in the seedling plots described below.

Tree seedlings (<1.4 m height) were recorded with two separate field sampling protocols. Tree seedling abundance was recorded by species in two 2 m^2 subplots in each plot in summer 1995–1997 and 2001. Multiple sprouts from an individual rootstock were recorded as one seedling. The 2 m^2 subplots were positioned along the hypotenuse of the sapling subplot, at one-third (11.8 m) and two-thirds (23.6 m) distance. However, the small sample area resulted in inadequate data for most species and recorded few seedlings >30 cm height.

In 2002, a much larger area per plot was sampled to record post-treatment seedling abundances. On each plot we sampled large seedlings (30–140 cm height) of all species along four 25 m long × 1.5 m wide belt transects (sample area = 150 m^2), spaced 5 m apart and located on one-half of the 50 m × 25 m vegetation plot. These transects had been established to sample the herbaceous vegetation (Hutchinson et al., 2005). Along each transect we recorded the abundance of oak and hickory seedlings by species in sixteen 4 m^2 quadrats (sample area = 64 m^2). The abundance of all non-oak + hickory seedlings was recorded in sixteen 1 m^2 quadrats (sample area = 16 m^2), nested within the 4 m^2 quadrats (sample area = 16 m^2). The quadrats were positioned at the 16 herbaceous-layer quadrat locations (Hutchinson et al., 2005). Multiple sprouts from a single rootstock were recorded as one seedling.

2.4.2. Canopy cover

Hemispherical photographs were taken in mid-summer 1995–1997 and in 1999. One photograph was taken at the center of each 50 m × 25 m plot 1.5 m above the forest floor. On these same forest sites, Robison and McCarthy (1999) showed no significant difference in canopy cover estimates between camera heights of 30 cm and 1.5 m. From 1995 to 1997, color slide photographs were taken with a Nikon FG-20 35 mm camera fitted with a Sigma 8 mm fisheye lens.

The 1999 photographs were taken with a Nikon Coolpix 950 digital camera fitted with a FC-E8 fisheye lens. The 1995–1997 images were analyzed with GLI/C Color Fish-Eye Photo Analysis, v. 3.1 (Canham, 1995) and the 1999 photographs were analyzed with Gap Light Analyzer (GLA), v. 2.0 (Frazer and Canham, 1999). Innouye (2000) showed that results from the two software algorithms were very strongly correlated. The analysis provides estimates of canopy openness (inverse = canopy cover), direct beam radiation, diffuse beam radiation, and total radiation.

2.5. Data analysis

We used a mixed linear model with repeated measures to test for significant treatment effects on overstory density and basal area, sapling density, canopy openness, and seedling density (PROC MIXED, SAS Institute, 1999). We used the autoregressive covariance structure. The four study sites were treated as random block effects and fire treatment and IMI were fixed effects. Pre-treatment (1995) data were used as the covariate to test for post-treatment effects of fire, IMI, fire × IMI, fire × year, IMI × year, and fire × IMI × year. The model did not test for the significance of site (block) effects. If overall F-tests were significant ($P < 0.05$) then least squares means (LS-means) tests were used to determine significant differences ($P < 0.05$) among treatments within each year. We used a mixed model without repeated measures to test for significant effects of fire treatment, IMI, and fire × IMI on paint tag temperatures and on large seedling abundance in 2002.

For 1995–2001 tree seedling abundances, which were sampled in only two small quadrats, we combined data from several species to form species groups thus reducing the number of plots containing zero abundance. We combined all tree species other than *A. rubrum* that were shade-tolerant and capable of obtaining overstory stature as "shade-tolerant overstory". Shade-tolerant species were those classified as either shade-tolerant or very shade-tolerant by Burns and Honkala (1990). We included *Fraxinus americana* in this group because it is shade-tolerant in the seedling stage despite being classified as intolerant overall (Burns and Honkala, 1990). In addition, we combined all *Quercus* and *Carya* seedlings into "oak + hickory". Similarly, for the analysis of large seedlings in 2002, which were often low in abundance despite the large sample area, we combined all shade-tolerant overstory species (including *A. rubrum*) into one group and all oaks and hickories into a separate group.

Simple linear regression was used to analyze the relationship between fertility and moisture and *Quercus* seedling abundance in 2002. To express fertility and moisture, we developed a relative fertility-moisture index, calculated from four equally weighted variables. Previous work on these study sites indicated that, in addition to the IMI, nitrogen mineralization rate, nitrification rate, and pH were strongly related to species composition (Hutchinson et al., 1999). We used the pre-treatment soil data which was reported in Morris and Boerner (1998) and Boerner et al. (2003). Each variable, including the IMI, was scaled from 0 to 1 based on the minimum and maximum values for all 108 plots. The mean of the four variables was calculated to obtain a fertility index value for each plot. Overall, the fertility index averaged 0.38 ± 0.03 and ranged from 0.07 to 0.85 across all plots.

3. Results

3.1. Fire intensity

In 1996, the first year of fire treatments, the mixed model indicated a significant IMI effect on paint tag temperatures ($F_{2,12} = 6.7$, $P = 0.01$) but no significant difference between designated treatment units ($F_{1,3} = 1.44$, $P = 0.32$). Xeric plots had higher mean temperatures (137 °C) than both intermediate (104 °C) and mesic (84 °C) plots (Fig. 2a). In 1997 and 1998, on the 4× units, temperatures averaged 84 and 132 °C, respectively; in both years, the IMI effect was not significant. In 1999, there was a significant fire treatment effect ($F_{1,3} = 11.2$, $P = 0.04$) as the 2× burn units, after 2 fire-free years, had significantly higher mean temperatures (166 °C) than the 4× units (112 °C) (Fig. 2b).

3.2. Fire effects on overstory trees

The mixed model indicated no significant fire ($F_{2,6} = 0.65$, $P = 0.56$) or fire × year ($F_{4,54} = 1.50$,

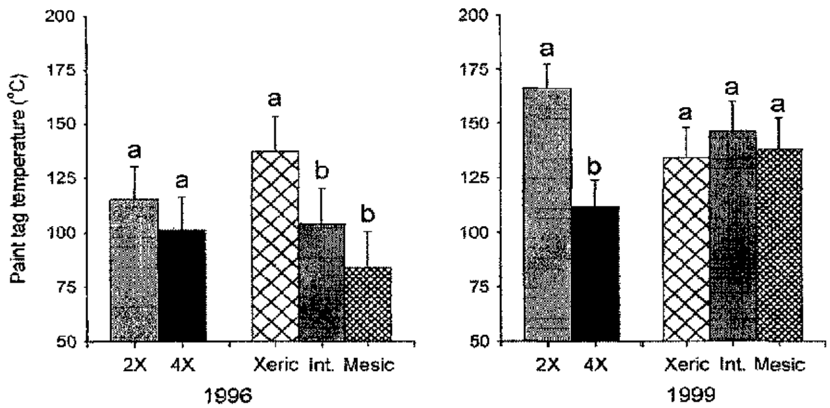

Fig. 2. Paint tag temperatures among fire treatment units (burned 2× and burned 4×) and IMI classes (xeric, intermediate, and mesic). Bars show least squares means (±1 S.E.) from mixed model output. Significant differences ($P < 0.05$) between fire treatments or IMI classes are indicated by different letters above the bars.

$P = 0.21$) effects on large tree (>25 cm DBH) density. Large tree density averaged 168–175 ha^{-1} for all treatments in all 3 post-treatment sample years (1997, 1999, and 2002). Tree basal area (BA) exhibited a significant fire × year effect ($F_{4,54} = 6.7$, $P < 0.01$). However, BA differences among treatments were very small in magnitude; by 2002, mean BA ranged from 28.8 m^2/ha on unburned units to 27.0 m^2/ha on 2× burn units.

In contrast to large trees, small tree (10–25 cm DBH) density exhibited a significant fire × year effect ($F_{4,54} = 7.81$, $P < 0.0001$) as 2× burn units had fewer small trees than both unburned and 4× burn units in 1999 and 2002 (Fig. 3a). By 2002 small tree density averaged 190 ha^{-1} on unburned units, 171 ha^{-1} on 4× units, and 138 ha^{-1} on 2× burn units. Among the two major tree groups, there were significant fire × year effects on shade-tolerant tree density ($F_{4,54} = 8.07$, $P < 0.0001$) and also oak + hickory density ($F_{4,54} = 2.61$, $P = 0.046$). By 2002, small shade-tolerant trees were significantly less abundant on 2× burn units (89 ha^{-1}) than on both 4× (111 ha^{-1}) and unburned (128 ha^{-1}) units (Fig. 3c). There was also a significant IMI effect ($F_{2,18} = 4.22$, $P = 0.03$) on the density of small shade-tolerant trees as mesic plots were more dense than xeric plots each year (Fig. 3d). In 2002, small oak + hickory trees were significantly less abundant on 2× units (43 ha^{-1}) than on both the 4× (55 ha^{-1}) and unburned (56 ha^{-1}) units (Fig. 3e). There were no significant effects of IMI, fire × IMI or fire × IMI × year on total small tree density (Fig. 3b) or on oak + hickory density (Fig. 3f).

Small tree mortality (1995–2002) varied substantially among the most abundant species, *A. rubrum*, *Q. alba*, *A. saccharum*, *Carya* spp., *Q. prinus*, and *N. sylvatica* (Fig. 4). Mortality was highest for all six species on the 2× burn units. *Q. alba* exhibited the highest mortality on both the unburned (18.1%) and 2× burn units (45.5%) and mortality was also relatively high on the 4× burn units (28.1%). *Q. prinus* had the second-highest mortality on unburned units (15.5%), but its mortality was less than one-half that of *Q. alba* on both the 2× (21.4%) and 4× (10.9%) units.

A. rubrum, the most abundant tree in the 10–25 cm DBH class, exhibited high mortality on the 2× (43.4%) and 4× (28.2%) burn units, but in contrast to the oaks, its mortality was much lower on unburned units (3.6%). Both *A. saccharum* and *N. sylvatica* mortality were relatively low across all treatments, <5% on unburned units, <10% on the 4× burn units, and <20% on the 2× burn units. *Carya* spp. mortality was much higher on the 2× burn units (28.7%) than on both the unburned and 4× burn units (<10%). By subtracting mortality on unburned units from that on the burn units (2× and 4× combined) the "fire-induced" mortality for each species was *A. rubrum* = 33%; *Q. alba* = 17%; *Carya* spp. = 13%; *N. sylvatica* = 10%; *A. saccharum* = 4%; *Q. prinus* = 2%.

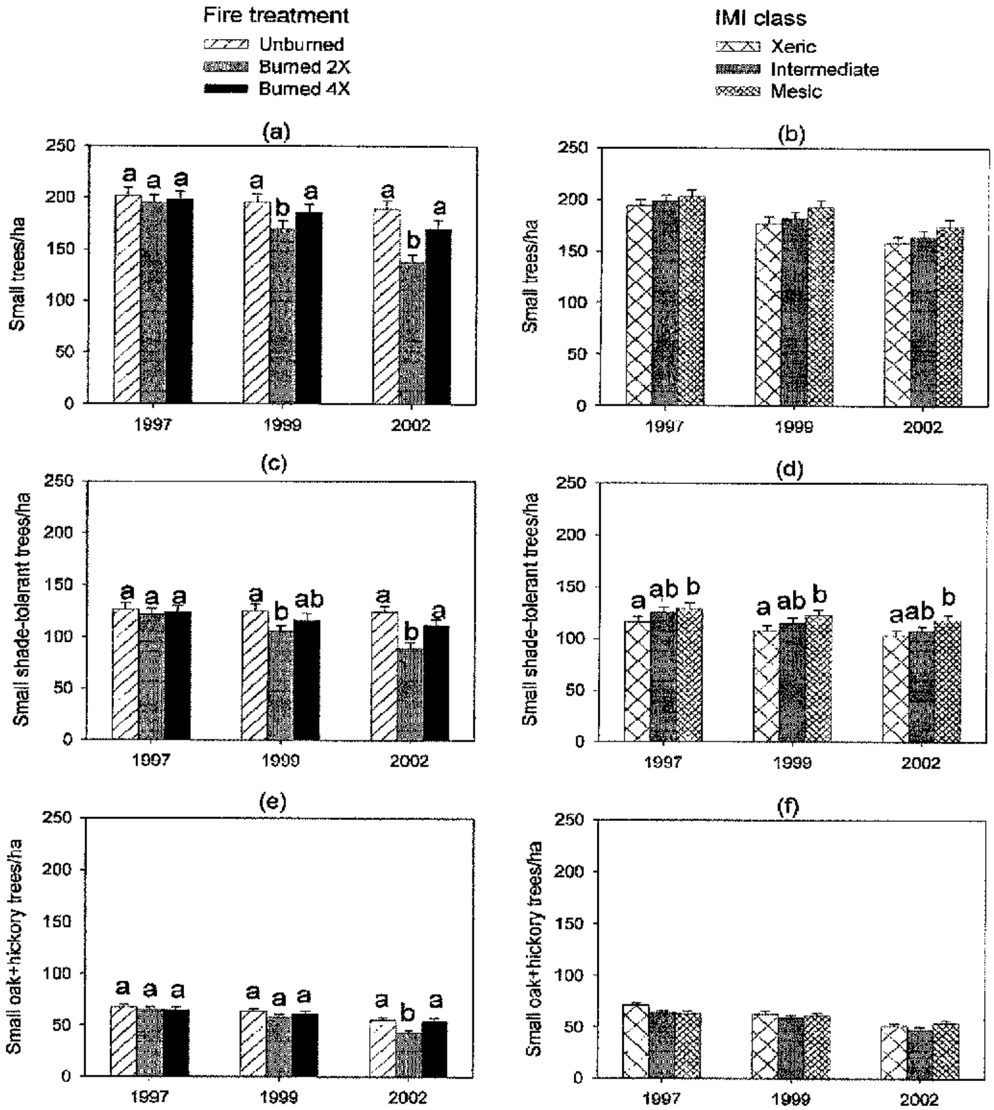

Fig. 3. Post-treatment small tree (10–25 cm DBH) density for (a) all trees, (b) shade-tolerant species, and (c) oak + hickory species. Bars indicate least squares means (±1 S.E.) adjusted by pre-treatment values as covariates from the mixed model. Significant annual differences ($P < 0.05$) between fire treatments or IMI classes are indicated with different letters above the bars, only if fire or IMI effects (or interactions) were significant.

3.3. Fire effects on saplings

The density of tree saplings, the great majority of which were shade-tolerant species, was reduced substantially by fire (Fig. 5). The mixed model indicated significant effects of fire ($F_{2,6} = 93.06$, $P < 0.0001$) and fire × year ($F_{4,108} = 2.44$, $P = 0.02$) on the density of small saplings (1.4 m height to 2.9 cm DBH). In all post-treatment years, small sapling density was much lower on burned units than on unburned units. After the first fires in 1996, small sapling densities had been reduced to a mean of

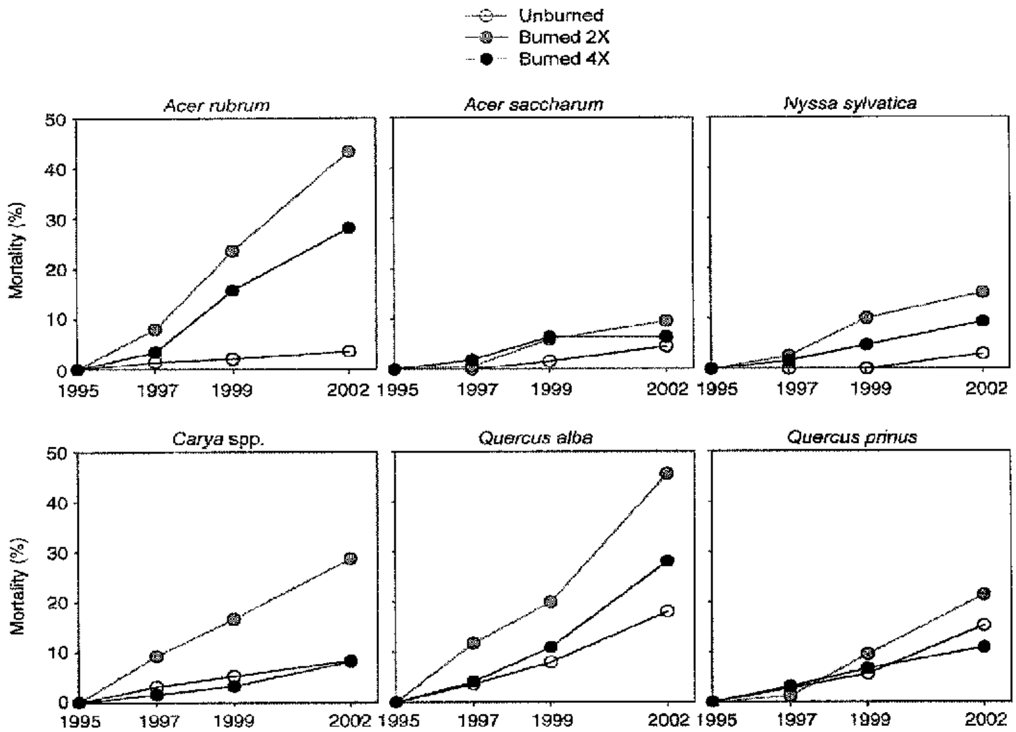

Fig. 4. Mortality of the six most abundant species in the small tree size class (10–25 cm DBH), among fire treatments. Mortality percentage was calculated from all of the trees present in 1995 before treatments began. The total number of trees in 1995 were *Acer rubrum* = 669, *A. saccharum* = 363, *Nyssa sylvatica* = 213, *Carya* spp. = 264, *Quercus alba* = 394, and *Q. prinus* = 220.

<500 ha^{-1} on both burn units, compared to >1500 ha^{-1} on unburned units (Fig. 5a). Small sapling densities were lowest on the burn units in 1999, averaging 139 and 55 ha^{-1} on the 2× and 4× burn units, respectively. Small sapling density also decreased by 34% on unburned units. This decrease was largely the result of *Cornus florida* mortality caused by the dogwood anthracnose fungus (*Discula destructiva*), first observed on the sites in 1995. Small *C. florida* sapling density decreased from a mean of 499 ha^{-1} in 1995 to 21 ha^{-1} in 2002 on unburned units, a 96% decline. There were no significant IMI effects or IMI interactions on small sapling density (Fig. 5b).

Large sapling (3.0–9.9 cm DBH) density exhibited significant fire ($F_{2,6} = 18.78$, $P = 0.003$) and fire × year ($F_{4,108} = 5.48$, $P < 0.0001$) effects. Large sapling densities were significantly lower on both burn treatments relative to unburned units each post-burn year (Fig. 5c). By 2002, mean densities were 495 ha^{-1} on unburned, 167 ha^{-1} on 2×, and 162 ha^{-1} on 4× burn units. There was also a significant IMI × year effect ($F_{8,108} = 2.4$, $P = 0.038$) on large sapling density; by 2002, large saplings were more abundant on mesic plots than on intermediate plots (Fig. 5d).

3.4. Canopy openness

There was a significant fire × year effect ($F_{6,81} = 2.37$, $P = 0.04$) on canopy openness. However, essentially closed-canopy conditions persisted as canopy openness averaged <6% for all treatments 1996–1999 (Fig. 6a). In 1999, open sky was significantly lower on unburned units than on 2× burn units. There was a significant IMI effect ($F_{2,18} = 4.75$, $P = 0.02$) on canopy openness as xeric

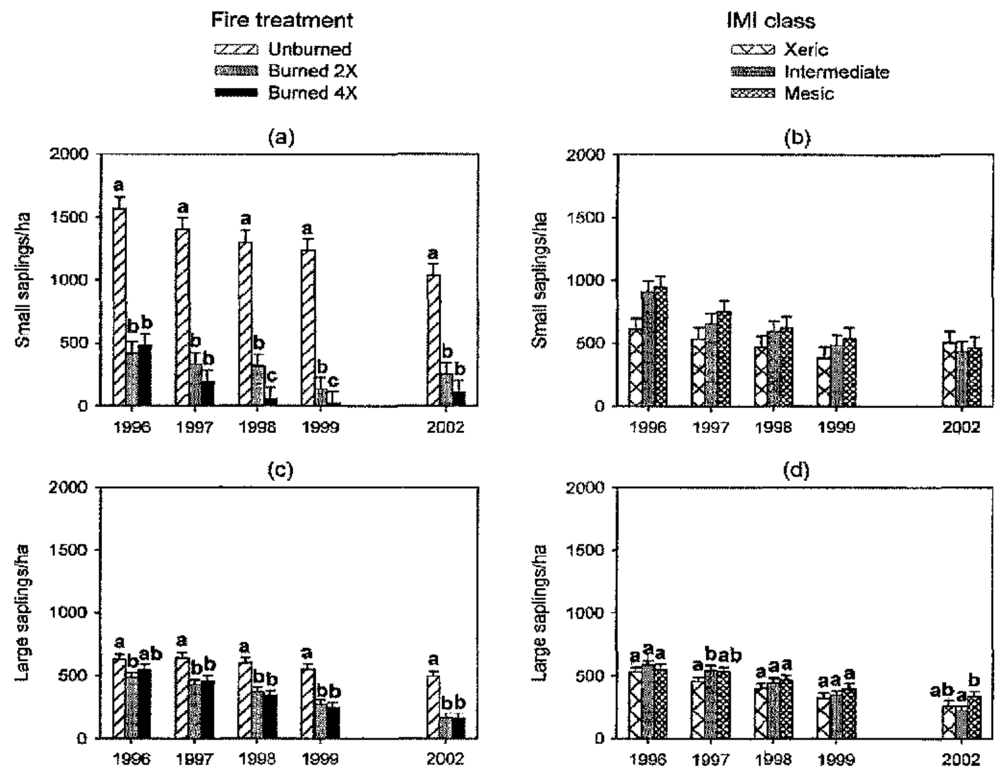

Fig. 5. Post-treatment densities of (a) small saplings, 1.4 m height to 2.9 cm DBH and (b) large saplings, 3.0–9.9 cm DBH. Bars indicate least squares means (±1 S.E.) adjusted by pre-treatment values as covariates from the mixed model. Significant annual differences ($P < 0.05$) are indicated by different letters above the bars, only if fire or IMI effects (or interactions) were significant.

plots had significantly more open sky than intermediate and mesic plots in 1997 (Fig. 6b).

3.5. Tree seedling abundance, 1995–1997, 2001

On the small permanent subplots, the mixed model indicated significant fire ($F_{2,6} = 9.17$, $P = 0.02$) and fire × year ($F_{4,54} = 8.41$, $P < 0.0001$) effects on *A. rubrum* seedling abundance. In both 1996 and 1997, *A. rubrum* density was significantly lower on both burn treatments compared with unburned units (Fig. 7a). However, by 2001, after 2 fire-free years on both burn units, *A. rubrum* abundance had increased on these units. In 2001 there was no significant difference among treatments as mean abundances ranged from 20,566 to 22,285 ha^{-1} among treatments. Seedling abundances of the other major shade-tolerant species combined (*A. saccharum*, *F. americana*, *N. sylvatica*, and *Ulmus rubra*) did not exhibit significant fire ($F_{2,6} = 0.45$, $P = 0.66$) or fire × year effects ($F_{4,54} = 1.88$, $P = 0.13$) (Fig. 7c). There was a significant IMI effect ($F_{2,18} = 3.84$, $P = 0.04$) on the density of shade-tolerant seedlings; in 2001, these were significantly less abundant on xeric plots than on intermediate and mesic plots (Fig. 7d). Oak + hickory seedling abundance exhibited non-significant fire ($F_{2,6} = 0.69$, $P = 0.54$) and fire × year ($F_{4,54} = 2.35$, $P = 0.25$) effects. Following abundant acorn production in autumn 1996, mean oak + hickory seedling abundances increased across all treatments, from 7635 to 14,029 ha^{-1} on unburned units, from 6088 to 15,583 ha^{-1} on 2× burn units, and from 8011 to 11,568 ha^{-1} on 4× burn units even as prescribed fires were conducted the following spring (Fig. 7e). From

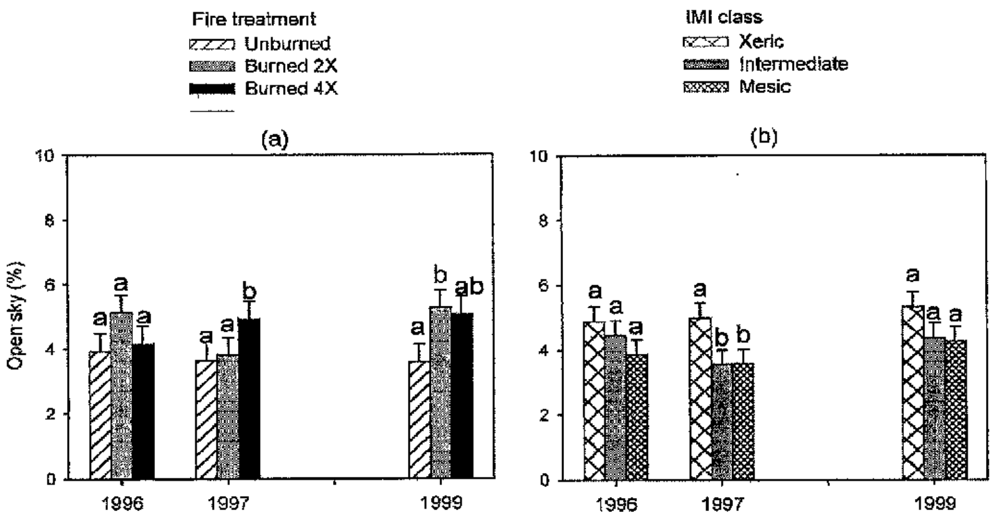

Fig. 6. Post-treatment open sky estimates among (a) fire treatments (burned 2× and burned 4×) and (b) IMI classes (xeric, intermediate, and mesic). Bars indicate least squares means (±1 S.E.) adjusted by pre treatment values as covariates from the mixed model. Significant annual differences ($P < 0.05$) are indicated by different letters above the bars, only if fire or IMI effects (or interactions) were significant.

1997 to 2001, the 2× burn units exhibited the largest decrease in mean oak + hickory seedling abundance, from 15,583 to 9083 ha^{-1}. The seed-banking *Liriodendron tulipifera* exhibited significant fire × year effects ($F_{4,54} = 6.88$, $P < 0.0001$). Abundant post-fire germination produced much greater *L. tulipifera* densities on burned units in 1996 (>40,000 ha^{-1}) and 1997 (>15,000 ha^{-1}) than on unburned units (<3000 ha^{-1}) (Fig. 7g). However, effects were ephemeral as all treatments averaged <2500 *L. tulipifera* seedlings/ha by 2001. Effects of IMI and interactions with IMI were not significant for oak + hickory and *L. tulipifera* (Fig. 7f and h).

3.6. Tree seedling abundance, 2002

Regression analysis indicated that the abundance of *Quercus* seedlings (all size classes) in 2002 was inversely related to the fertility-moisture gradient ($r^2 = 0.40$, $P < 0.01$, Fig. 8). Along the fertility-moisture gradient, there is no visible separation of plots among the three fire treatments. Among treatments, *Quercus* seedling densities were: unburned = 3761 ± 587 ha^{-1}, burned 2× = 3271 ± 659 ha^{-1}, and burned 4× = 3439 + 682 ha^{-1}. Among sites, mean *Quercus* seedling densities were: WR = 4991 ± 827 ha^{-1}, AR = 4076 ± 617 ha^{-1}, YB = 3427 ± 901 ha^{-1}, and BR = 1467 ± 319 ha^{-1}.

For large oak + hickory seedlings (>30 cm height) in 2002, the mixed model indicated no significant fire effect ($F_{2,6} = 0.53$, $P = 0.62$; Fig. 9a). There was a significant IMI effect ($F_{2,18} = 9.07$, $P = 0.002$) on large oak + hickory seedling abundance as xeric plots had a mean of 1516 seedlings/ha, significantly higher than both intermediate (581 ha^{-1}) and mesic (443 ha^{-1}) plots. In 2002, 21 plots averaged >1000 large oak + hickory seedlings/ha. Nearly all of these plots were: (1) xeric or intermediate ($n = 19$), (2) on burned sites ($n = 18$), and (3) located at the WR and AR study sites ($n = 17$). On 33 plots, <100 large oak + hickory seedlings/ha were present and most of these plots were: (1) intermediate and mesic ($n = 31$) and (2) located at YB and BR study sites ($n = 25$). For the large shade-tolerant seedlings, both fire ($F_{2,6} = 0.62$, $P = 0.57$) and IMI ($F_{2,18} = 0.57$, $P = 0.57$) effects were non-significant. Across all treatments, large seedling abundances averaged 831 ha^{-1} for oak + hickory and 1014 ha^{-1} for shade-tolerant species.

The most abundant large seedling on xeric plots was *Sassafras albidum*, which averaged 2886 ha^{-1} (IMI effect: $F_{2,18} = 5.03$, $P = 0.02$). However, densities were highly variable and large seedlings were absent from

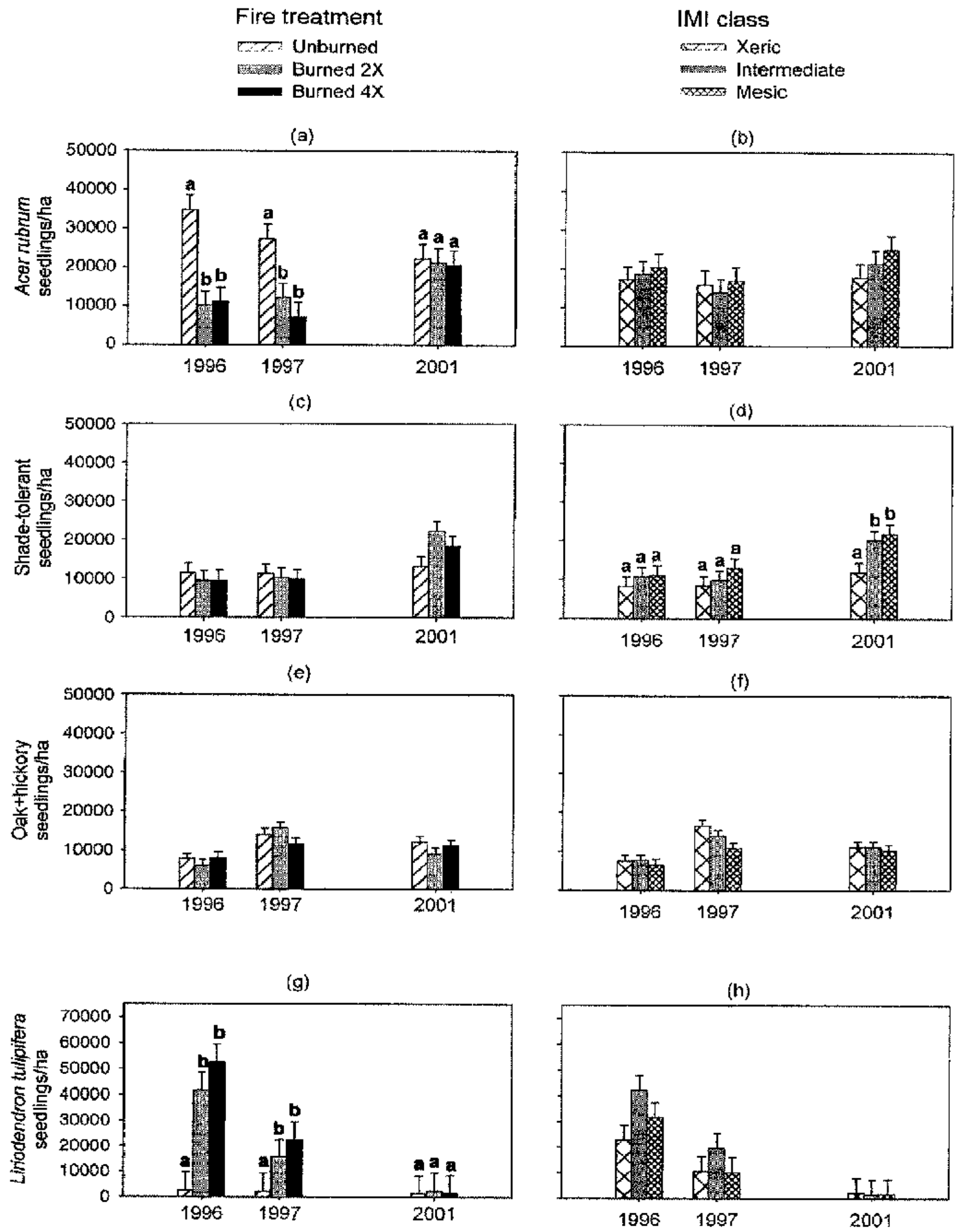

Fig. 7. Post-treatment densities of seedlings (all stems <1.4 m height) by species group, collected from two 2 m^2 subplots per vegetation plot ($n = 108$). The shade-tolerant group includes all shade-tolerant species other than *A. rubrum*. Bars indicate least squares means (±1 S.E.) adjusted by pre-treatment values as covariates from the mixed model. Significant annual differences ($P < 0.05$) are indicated by different letters above the bars, only if fire or IMI effects (or interactions) were significant.

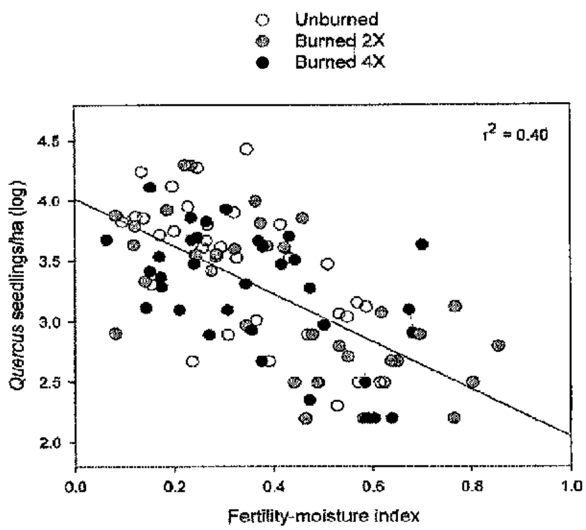

Fig. 8. Linear regression analysis of the fertility-moisture index and $\log_{10}$-transformed *Quercus* seedling abundance in 2002 (post-treatment). Plots are designated by fire treatment; $n = 104$ plots (four plots with no *Quercus* seedlings were excluded from the analysis).

one-half ($n = 54$) of all plots. For large *S. albidum* seedlings, fire ($F_{2,6} = 1.13$, $P = 0.38$) and fire × IMI ($F_{4,18} = 0.40$, $P = 81$) effects were non-significant though the highest densities usually occurred on xeric plots that had been burned.

4. Discussion

One objective of prescribed fire use in oak forests is to create more open-structured stands, thus improving the competitive status of oak seedlings versus shade-tolerant species (Lorimer et al., 1994; Johnson et al., 2002). A dense sapling layer of shade-tolerant species is considered an important limiting factor to the development of oak advance regeneration (Abrams, 1992, Johnson et al., 2002) and sapling-layer removal has been shown to significantly improve oak regeneration (Lorimer et al., 1994). In our study, both fire treatments caused large reductions in the density of saplings, nearly all of which were shade-tolerant species. Similar fire effects on the sapling layer of oak forests have been reported in other studies (Arthur et al., 1998; Elliott et al., 1999; Blake and Schuette, 2000). While nearly all saplings resprouted following topkill by fire, there was very little ingrowth of stems into the sapling layer in the 4 years that followed the last fires in 1999.

However, because the majority of small trees and nearly all large trees survived the fires, the canopy remained closed despite large reductions in sapling density. In Wisconsin oak forests, Lorimer et al. (1994) decreased canopy cover to a greater degree by the mechanical removal and herbicide treatment of the sapling layer, intended to simulate fire. In contrast with our relatively short-term study, frequent fire applied over a long-term period (>20 years) has been shown to promote and maintain much lower tree density in oak forests (Huddle and Pallardy, 1996) and savannas (Peterson and Reich, 2001).

Other short-term studies have shown that low-intensity fires have little effect on the overstory of oak forests (Elliott et al., 1999; Blake and Schuette, 2000; Franklin et al., 2003). However, high-intensity fires can cause significant mortality to larger trees. Regelbrugge and Smith (1994) found that basal area and overstory density were reduced by 67 and 81%, respectively, after a wildfire in Virginia mixed-oak stands. Moser et al. (1996) reported overstory density and basal area reductions of 60–95% after intense prescribed fires in Connecticut oak forests.

The thin-barked *A. rubrum* is considered fire sensitive and fire suppression is thought to have facilitated its widespread increase in historically oak-dominated landscapes (Lorimer, 1984; Abrams, 1998). In our study, *A. rubrum* mortality was relatively high on both burn treatments. It was also shown susceptible to fire by Harmon (1984) and Regelbrugge and Smith (1994). *A. saccharum* is also considered to be increasing in abundance because of fire suppression (Abrams, 1992). However, we found that *A. saccharum* mortality was very low on burned sites. Hengst and Dawson (1994) reported that *A. saccharum* bark thickness was similar to that of *Q. alba*. Though perhaps most important in our study was that 88% of small *A. saccharum* trees were located on only 19 of the 76 burn plots, which were generally sheltered, mesic sites that burned at low intensity. The mean maximum paint tag temperature on these 19 plots was much lower (137 °C) compared to the other 57 burn plots (179 °C). Also resistant to fire were *Q. prinus* and *N. sylvatica*, similarly reported by Harmon (1984) and Regelbrugge and Smith (1994).

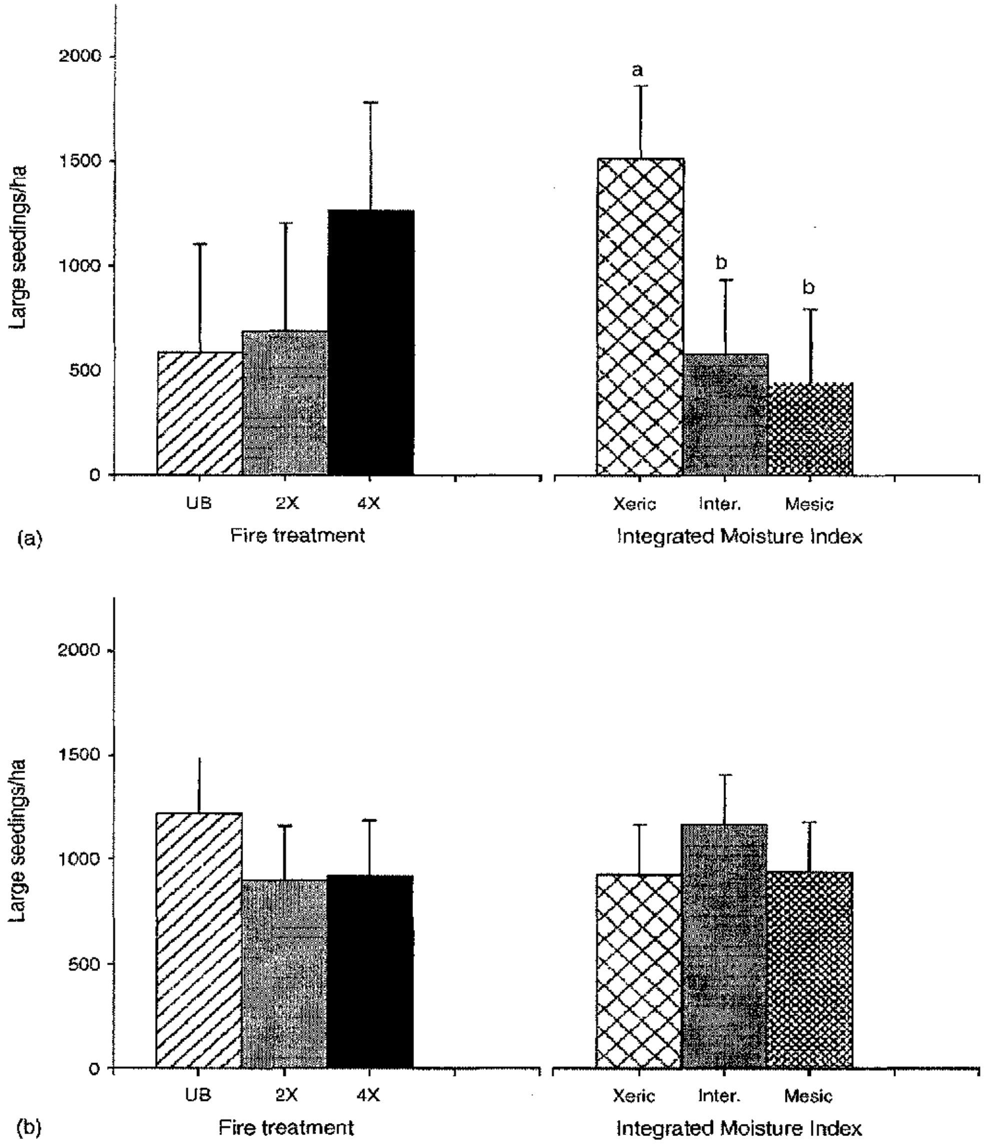

Fig. 9. Post-treatment (2002) abundance of seedlings 30–140 cm height among fire treatments (burned 2× and burned 4×) and IMI classes (xeric, intermediate, and mesic) for (a) all oak + hickory seedlings and (b) all shade-tolerant seedlings, among fire treatments and IMI classes. Bars indicate least squares means (±1 S.E.) from the mixed model. Significant differences ($P < 0.05$) among fire treatments and IMI classes are indicated by different letters above the bars, only if fire or IMI effects (or interactions) were significant.

Q. alba is considered well adapted to a regime of frequent low-intensity fires (Abrams, 2003). However, small *Q. alba* trees exhibited mortality rates on burn units that were similar to *A. rubrum*. High mortality of *Q. alba* could be related to several factors. First, mortality of small *Q. alba* trees was high on unburned plots. These suppressed midstory trees may have been more susceptible to fire damage because of poor vigor, possibly exacerbated by summer drought conditions in 1999. In addition, the smooth patch fungus *Aleurodiscus oakesii* is common on *Q. alba* in these study sites (Robert Long, personal communication). The fungus decomposes outer layers of dead bark (Sinclair et al., 1987), and has been shown to reduce bark thickness in *Q. muehlenbergii*, presumably reducing fire resistance (Hengst and Dawson, 1994).

The tree seedling data in this study was limited, reducing our ability to detect change over time. First, the area sampled in the small permanent subplots (4 m^2/plot) was inadequate for most individual seedling species and for large seedlings (>30 cm height). The area sampled was greatly increased in 2002, but these data only provide post-treatment comparisons. Second, we lacked demographic data on individual seedlings (e.g., survivorship, sprouting, and germination). Despite these limitations, large treatment effects were detected statistically. From both seedling data sets, we conclude that fire did not alter the competitive status of oak + hickory seedlings relative to that of shade-tolerant seedlings in either a consistent or substantial manner.

The initial large decrease in *A. rubrum* seedling abundance after fire was short-lived. Despite relatively high mortality of *A. rubrum* trees on burn units, it remained the most abundant midstory species. Seedling populations rapidly recovered, presumably from continued seed production and seedling establishment. Oak + hickory seedling abundance increased sharply after a large acorn crop in autumn 1996, following the first burns. However, fire effects on seedling densities after the large mast crop were not significant. This contrasted with the findings of Barnes and Van Lear (1998) and Brose and Van Lear (1998), both of whom showed that oak establishment improved after fire. Similar to our results, low-intensity dormant-season fires have most often shown relatively little effect on oak seedling populations (Arthur et al., 1998; Elliott et al., 1999; Franklin et al., 2003). However, the combined use of mechanical thinning and fire (Reich et al., 1990; Kruger and Reich, 1997; Brose and Van Lear, 1998) or high-intensity fire (Moser et al., 1996) have improved oak regeneration but not in all cases (Wendel and Smith, 1986; Franklin et al., 2003).

In 2002, the abundance of large oak + hickory seedlings in our study was much lower compared with that found by Brose and Van Lear (1998) after shelterwood harvests. They reported oak + hickory seedling densities ranging from 3000 ha^{-1} on unburned units to 5500 ha^{-1} on spring-burn units. In our study, large oak + hickory seedlings only approached their post-shelterwood abundances on the 4× burn sites at AR and WR (mean = 3444 ha^{-1}).

Our study was designed to contain four similar study sites (random block effect) and it was not an objective to test for significant differences among sites. However, even though overstory structure and composition were very similar among sites prior to treatments, there was variation among sites in the abundance of large oak + hickory seedlings. Plots that had the most large oak + hickory seedlings were located primarily at AR and WR, on dry and intermediate sites that had been burned. However, given our lack of pre-treatment data on large seedling densities, the greater abundances on AR and WR burn plots could result more from abundant pre-treatment advance regeneration, rather than more substantial fire effects on those sites.

Vegetation and soils are strongly related to the IMI in this topographically dissected landscape (Hutchinson et al., 1999). However, there were no significant fire × IMI or fire × IMI × year interactions in our temporal analyses. When fire effects were significant, the lack of IMI interactions indicates that fire effects were either similar or among the IMI classes or that variability was high. The lack of significant IMI effects may be at least partly attributable to the fact that fire intensity was fairly similar across the moisture gradient after the first fires in 1996.

After more than 60 years with little or no fire, maples and other shade-tolerant species have become abundant in the midstory and understory of these historically oak-dominated forests. Without some management, these species are poised to dominate in the future. Timber harvesting methods that remove all large oaks (e.g., diameter-limit harvests, clearcutting) or other factors, such as gypsy moth defoliation, can accelerate these successional trends (Abrams and Nowacki, 1992; Fajvan and Wood, 1996).

We detected no consistent fire effects on the relative abundance or size of oak seedlings as the understory remained largely shaded and shade-tolerant seedling establishment continued. Though our results do not provide a prescription for improved oak regeneration, there is some equivocal evidence that fires at least began a shift toward improved oak forest sustainability. The dense layer of shade-tolerant saplings, which can impede oak regeneration (Lorimer et al., 1994), was virtually eliminated on burned units. The higher intensity fires on the 2× burn units reduced the density of midstory trees. *A. rubrum*, the most abundant and widely distributed midstory species, was susceptible to fire, contrasting with the fire-resistant *Q. prinus* and the moderately fire-resistant *Carya* spp.

Though annual burns were operationally feasible, we found that burning at intervals of at least 2–3 years can result in greater fire intensity, which in turn can open stand structure to some extent via midstory thinning. Fire seasonality also could be an important factor in determining fire effects. In our region from mid- to late-April, maples have translocated more carbohydrate reserves upward for leaf expansion and development than have oaks and hickories. Fires conducted during this later period would likely have a greater impact by further decreasing the sprouting capacity of maples relative to oaks and hickories (Brose and Van Lear, 1998).

In managed oak forests, studies have shown that the combined use of partial timber harvests (e.g., thinning, shelterwood, and group-selection) with the use of fire are more likely to improve oak regeneration in the short term, particularly on relatively mesic landscape positions (e.g., Kruger and Reich, 1997; Brose and Van Lear, 1998). In oak forests where harvesting is not permitted or desirable (e.g., preserves, recreation areas) our results suggest that longer term prescribed fire application eventually could promote and sustain more open-structured and presumably more sustainable oak forests. Periodic fires (e.g., 2–5-year intervals) of moderately high intensities applied over 20 years or more likely would result in more substantial midstory thinning, particularly of the most abundant but fire-sensitive *A. rubrum*. It is likely that one or more fires would be sufficiently intense to kill some overstory trees, further opening stand structure. For example, a 2001 prescribed fire at the Vinton Furnace Experimental Forest caused a 20% basal area reduction in high-intensity burn areas, which covered ~50% of a 20-ha burn unit (Yaussy, unpublished data). However, our results suggest that even long-term burning may be insufficient to reduce midstory density on more sheltered sites where *A. saccharum* is abundant in the midstory.

In a longer term burning regime, periodic fires could maintain canopy openings caused by windthrow and natural mortality by preventing shade-tolerant species from filling the gaps. In Wisconsin oak savannas, Peterson and Reich (2001) found that frequent fires (≥3 per decade) conducted over a 32-year period prevented the development of a dense sapling layer. These longer term openings, with increased light levels, should favor the development of oak advance regeneration (e.g., Rebertus and Burns, 1997), which can sprout repeatedly following topkill.

Studies of prescribed fire, such as ours, often have limited flexibility as to the timing and frequency of burns. However, managers can use prescribed fire more adaptively, maximizing the benefits it may provide. For example, burning could be limited to years when weather conditions and fuels permit moderate to high fire intensity, in order to reduce stand density. Fires should also be coordinated with acorn production. Following a large mast year, new oak seedlings should be allowed several fire-free years in order to develop sufficient belowground reserves for sprouting after the next fire.

There has long been speculation over the role of fire in oak ecosystems (e.g., Cottam, 1949). However, we still know surprisingly little about whether long-term prescribed fire application can restore oak forest structure and sustainability. As studies, such as ours, are continued, we will understand more about the efficacy of using prescribed fire to sustain eastern oak forests. Our multidisciplinary study has shown that prescribed fire application can have other beneficial short-term effects, including the amelioration of acidic deposition (Boerner et al., 2004), increasing native plant diversity (Hutchinson et al., 2005), and sustaining rare plant populations (Hutchinson, 2004).

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