Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests

Todd F. Hutchinson, Robert P. Long, Joanne Rebbeck, Elaine Kennedy Sutherland, and Daniel A. Yaussy

Abstract: Oak dominance is declining in the central hardwoods region, as canopy oaks are being replaced by shade-tolerant trees that are abundant in the understory of mature stands. Although prescribed fire can reduce understory density, oak seedlings often fail to show increased vigor after fire, as the canopy remains intact. In this study, we examine the response of tree regeneration to a sequence of repeated prescribed fires followed by canopy gap formation. We sampled advance regeneration (stems >30 cm tall) in 52 gaps formed by synchronous mortality of white oak (*Quercus alba* L.); 28 gaps were in three burned stands and 24 gaps were in three unburned stands. Five years after gap formation, unburned gaps were being filled by shade-tolerant saplings and poles and were heavily shaded (7% of full sun). By contrast, tolerant saplings had been virtually eliminated in the burned gaps, which averaged 19% of full sun. Larger oak and hickory regeneration was much more abundant in burned gaps, as was sassafras, while shade-tolerant stems were equally abundant in burned and unburned gaps. Our results suggest that the regeneration of oak, particularly that of white oak, may be improved with multiple prescribed fires followed by the creation of moderate-sized canopy gaps (200–400 m^2).

Résumé : La dominance des chênes diminue dans la région centrale de la forêt feuillue et son couvert est graduellement remplacé par celui d'arbres tolérants à l'ombre qui sont abondants dans le sous-bois des forêts matures. Bien que le brûlage dirigé puisse réduire la densité des arbres du sous-bois, les semis de chêne sont souvent incapables d'augmenter leur vigueur après feu lorsque la canopée demeure intacte. Dans cette étude, nous évaluons la réaction de la régénération des arbres à la suite de brûlages dirigés répétés qui ont précédé la formation de trouées dans la canopée. Nous avons échantillonné la régénération préétablie (plus de 30 cm de hauteur) dans 52 trouées formées par la mort synchrone de chênes blancs (*Quercus alba* L.). Vingt-huit trouées étaient situées dans trois peuplements brûlés alors que 24 trouées étaient situées dans trois peuplements non brûlés. Cinq ans après la formation des trouées, les trouées des peuplements non brûlés étaient occupées par des gaules et des perches d'espèces tolérantes à l'ombre et étaient fortement ombragées (7 % de la pleine lumière). À l'inverse, les gaules d'espèces tolérantes à l'ombre avaient été pratiquement éliminées des trouées des peuplements brûlés qui recevaient, en moyenne, 19 % de la pleine lumière. Une régénération de grande taille de chêne et de caryer était beaucoup plus abondante dans les trouées des peuplements brûlés, tout comme le sassafras, alors que les individus tolérants à l'ombre étaient aussi abondants dans les trouées des peuplements brûlés que non brûlés. Nos résultats indiquent que la régénération du chêne, particulièrement celle du chêne blanc, peut être améliorée à l'aide de brûlages dirigés multiples, suivis par la création de trouées de taille modérée (de 200 à 400 m^2) dans la canopée.

[Traduit par la Rédaction]

Introduction

In addition to climate and landform, disturbance regime is a key factor in determining the structure, species composition, and dynamics of forest ecosystems. In many regions, altered disturbance regimes have led to undesirable changes in forest composition (Abrams 2003; Royo and Carson 2006). With the recognition that natural and anthropogenic disturbances have shaped the development of forest ecosystems, management strategies increasingly seek to restore or emulate a disturbance regime that will produce the desired condition (Attiwill 1994).

The Central Hardwoods Forest Region of the eastern United States, comprising more than 1.4 million km^2, is characterized by the dominance of oaks (*Quercus* L. spp.) (Fralish 2003). However, throughout much of the region, canopy oaks are often replaced by nonoak species on all but the driest sites (e.g., site index <18 m; Lorimer 1993). Substantial decreases in oak dominance have been documented when natural canopy gaps are formed (Cho and Boerner 1991) and after timber harvesting (Jenkins and Parker 1998). Poor oak regeneration after a disturbance occurs when the abundance, and particularly the size, of oak seedlings (advance reproduction) is insufficient to compete with well-established saplings

Received 16 September 2011. Accepted 1 December 2011. Published at www.nrcresearchpress.com/cjfr on xx January 2012.

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and poles of shade-tolerant species or newly established but fast-growing shade-intolerant species (Loftis 2004).

There is growing evidence from studies of fire-scarred trees that anthropogenic fires occurred periodically (return intervals generally 5–15 years) at a number of sites in the central hardwoods region, before and after Euro-American settlement, until the onset of fire control policies in the early 20th century (e.g, Guyette et al. 2002; McEwan et al. 2007). The recurrent fires are thought to have sustained oak woodlands and forests by reducing competition from less fire-adapted species (Abrams 1992), and dendrochronology studies have shown a direct association between the cessation of fire and a shift from the recruitment of oaks to other species (Shumway et al. 2001; Hutchinson et al. 2008).

In attempts to improve regeneration outcomes for oak and the ecologically similar hickory (*Carya* Nutt. spp.), a variety of management approaches are being tested and implemented (Brose et al. 2008), including the combined use of prescribed fire and partial harvesting. Partial harvests and (or) herbicide treatments, typically in a shelterwood system, can promote the development of oak advance reproduction by increasing light to the forest floor while limiting the dominance of shade-intolerant species such as yellow-poplar (*Liriodendron tulipifera* L.) (Loftis 1990; Johnson et al. 2002). Prescribed fire is used in conjunction with these treatments to improve the competitive status of oak advance reproduction. Oak seedlings, if large enough, sprout vigorously after topkill by fire from belowground carbohydrate reserves developed by their "root-centered" growth strategy (Johnson et al. 2002; Brose and Van Lear 2004).

Several studies of tree regeneration in mixed-oak forests have examined the combined treatments of partial timber harvest and prescribed fire. Results suggest that a number of factors, including site quality, stand composition, and the timing and intensity of treatments, affect regeneration outcomes. The competitive status of oak regeneration was shown to decrease when partial harvests were followed immediately (within 1 year) by a single prescribed fire in West Virginia (Wendel and Smith 1986) and southern Ohio (Albrecht and McCarthy 2006). In these studies, vigorous sprouting by competitors (e.g., red maple (*Acer rubrum* L.), striped maple (*Acer pensylvanicum* L.), flowering dogwood (*Cornus florida* L.), and sassafras (*Sassafras albidum* L.)) or rapid growth of newly established seedlings (e.g., yellow-poplar) outpaced the development of oak advance regeneration. In mesic oak stands in Wisconsin, the competitive status of northern red oak (*Quercus rubra* L.) regeneration was enhanced relative to that of sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) in stands that were burned twice after canopy openings were created (Kruger and Reich 1997). Brose and Van Lear (1998), in the Virginia Piedmont, showed that a single prescribed fire conducted several years after a shelterwood harvest (to 50% residual basal area) increased the competitive status of oak regeneration relative to the major competitors (yellow-poplar, red maple). The single prescribed fire was most beneficial to oak regeneration when conducted during the growing season and at relatively high intensity, results that were reaffirmed 12 years after the fires (Brose 2010). Each of these studies examined the effects of one or two prescribed fires that were conducted after a partial harvest or the creation of moderate-sized openings.

Only a few studies in oak forests have examined the effects of repeated prescribed fires on tree regeneration over relatively long time periods (>10 years). These studies, which were conducted in mature oak forests and did not include timber harvesting, failed to show a substantial improvement in the competitive status of oak regeneration (Blankenship and Arthur 2006; Alexander et al. 2008). To date, there has been no research in oak forests documenting the response of tree regeneration to a sequence of multiple prescribed fires followed by canopy gap formation.

A regional white oak (*Quercus alba* L.) decline, characterized by the death of one to several overstory trees in discrete patches, became apparent in southern Ohio in 2003. The white oak decline provided a unique opportunity to compare tree regeneration in canopy gaps within stands that had been burned repeatedly prior to gap formation with that in gaps located in unburned stands. The primary objective of this study was to compare the structure, composition, and abundance of tree regeneration in burned and unburned gaps and, more specifically, to determine whether the competitive status of oak and hickory regeneration was greater in burned gaps than in unburned gaps. We also sought to compare gap attributes (gap area, the number and size of dead trees per gap, percentage of full sunlight, and the density of saplings and poles) in burned and unburned stands and to determine how these factors, as well as the topographic moisture regime, were related to the abundance of oak and hickory regeneration.

Methods

Study area

In 1995, we began a long-term study, located in southern Ohio, to examine the effects of prescribed fire on oak forest ecosystems (Sutherland and Hutchinson 2003). The study area is located in Vinton County, Ohio, in the Vinton Furnace State Experimental Forest (VFSEF) (39°11′N, 82°22′W). The VFSEF lies within the unglaciated Allegheny Plateau of southern Ohio. Mean annual temperature is 11.3 °C and precipitation averages 1024 mm and is distributed evenly throughout the year. Sandstones and shales are principal bedrocks. Topography is dissected, with narrow ridges and steep slopes; elevation ranges from 220 to 300 m. Soils are well-drained acidic silt and sandy loams of the Gilpin–Germano–Steinsburg series (Lemaster and Gilmore 2004). Site index for black oak (*Quercus velutina* Lam.) typically ranges from 17 m on ridgetops and upper south-facing slopes to 25 m on lower north-facing slopes (Carmean 1965). Original land surveys in the region (ca. 1800) indicate that upland forests were dominated by oaks and hickories, with white oak comprising nearly 30% of witness trees (Dyer 2001).

In the mid- to late 1800s, stands throughout the VFSEF were clearcut to provide charcoal for the iron industry. Dendrochronology studies in the VFSEF indicate that, within stands, fires occurred every 6–9 years, from ca. 1875 to 1935, as the young forests were redeveloping after clearcutting (Sutherland 1997; McEwan et al. 2007; Hutchinson et al. 2008). After 1935, fires rarely occurred, as fire control became effective throughout southern Ohio.

The overstory of present-day upland forests at VFSEF is dominated by oaks, with the most abundant species being white oak, chestnut oak (*Quercus prinus* L.), and black oak. Hickories, primarily mockernut (*Carya tomentosa* (Poir.) Nutt.) and pignut (*Carya glabra* (Mill.) Sweet), are also common in the overstory. Yellow-poplar occurs frequently on mesic sites but is seldom dominant. In sharp contrast with the overstory, the midstory and particularly the sapling layer are dominated by shade-tolerant species. Similar stand conditions are common throughout much of southern Ohio (Widmann et al. 2009).

Mortality due to white oak decline (ca. 2003) occurred primarily on relatively mesic landscape positions (e.g., lower half of hillslopes, site index approximately 19–24 m). Multiple factors are thought to be related to the decline, including drought and insect defoliations followed by excess precipitation and attack by the root-rotting pathogen *Phytophthora cinnamomi* (Nagle et al. 2010).

Experimental design

We selected six stands in which to study the effects of prescribed fire on tree regeneration in canopy gaps (Table 1). Three stands had been burned with multiple (three to five) low-intensity prescribed fires from 1996 to 2005 and three stands were unburned. Five stands (three burned, two unburned) were part of the prescribed fire study begun in 1995 (see Sutherland and Hutchinson 2003), and the additional unburned stand had been established in 2000 as part of the national Fire and Fire Surrogates study. Data from permanent plots located within the six stands indicated that, prior to the prescribed fire treatments, all stands were similar in structure and were dominated by oaks and hickories in the overstory. The sapling layer was dominated by shade-tolerant species; the most abundant, in descending order, were red maple, blackgum (*Nyssa sylvatica* Marsh var. *sylvatica*), American beech (*Fagus grandifolia* Ehrh.), flowering dogwood, and sugar maple. The overall mean pretreatment abundance of oak plus hickory seedlings (all stems <1.4 m tall) was similar in unburned and burned stands but exhibited considerable variation within and among individual stands.

Prescribed fires were conducted almost exclusively in the spring dormant season when leaves of overstory and understory trees had not yet expanded; a single fire was in the fall dormant season (Table 2). Prescribed fires were ignited in strips and were generally low intensity with flame lengths <1 m. Although fires were low intensity, most of the landscape was burned (>85%) during each fire. By 2002, fires had altered stand structure primarily by reducing midstory and understory density and fire effects on stand structure were similar in all of the burned stands (Hutchinson et al. 2005). Therefore, we treat all three burned stands as simply “burned”, regardless of fire frequency. Among the burned stands, trees >25 cm diameter at breast height (DBH) (1.37 m) exhibited 5%–6% mortality from 1995 to 2002, trees 10–25 cm DBH experienced 19%–36% mortality, and the density of saplings (1.4 m tall to 9.9 cm DBH) had been reduced by 79%–86%.

In 2008, we selected 52 canopy gaps in six stands to document the abundance of tree regeneration. In all, 24 gaps were located in three unburned stands and 28 gaps were in three burned stands. All gaps were located ≥50 m from other gaps

Table 1. Pretreatment attributes (mean (range)) for the three unburned (UB) and three burned (3X, 5X) stands and the number of gaps sampled per stand in 2008.

		Overstory[a]		Saplings[b]		Seedlings[c]	
Stand	Area (ha)	Basal area (m^2/ha)	Oak plus hickory basal area (%)	Density (stems/ha)	Shade-tolerant density (%)	Oak plus hickory density (stems/ha)	Gaps sampled
Arch Rock UB	24	25.9 (21.1–31.1)	82.6 (70.5–100)	2005 (960–3456)	87.3 (26.2–100)	13778 (1500–30000)	12
Watch Rock UB	20	25.9 (21.4–28.7)	81.8 (62.4–96.4)	1668 (1056–2433)	96.4 (84.7–100)	5333 (1500–10000)	6
RM UB	23	27.6 (23.7–30.4)	82.4 (72.5–88.9)	2067 (1333–2333)	97.3 (88.0–100)	10000 (2000–21000)	6
Arch Rock 3X	24	27.2 (22.1–33.3)	90.5 (81.9–99.0)	1892 (576–3584)	95.8 (86.4–100)	10444 (1500–30000)	8
Arch Rock 5X	32	28.4 (21.2–35.2)	77.0 (37.8–95.6)	2140 (864–4570)	94.3 (81.8–100)	7000 (1500–27500	11
Watch Rock 5X	31	23.5 (17.4–28.6)	82.2 (46.0–98.6)	1788 (800–3008)	77.8 (44.4–98.1)	9778 (1500–27500)	9

Note: For the RM UB stand, data were collected in 2000 on ten 0.1 ha plots (see Waldrop et al. 2008). For all other stands, data were collected in 1995 on nine 0.125 ha plots per stand (see Hutchinson et al. 2005).

[a]Calculated from trees ≥10 cm DBH.

[b]Stems 1.4 m tall to 9.9 cm DBH.

[c]All stems <1.4 m tall.

Table 2. Dates of the 15 prescribed fires conducted in three stands.

Stand	1996	1997	1998	1999	2004	2005
Arch Rock 3X	18 April			26 March		15 April
Arch Rock 5X	19 April	2 April	6 April	26 March	17 April	
Watch Rock 5X	21 April	3 April	6 April	27 March	9 November	

to minimize correlation between gaps within stands. We selected only gaps that appeared to have been formed during the recent white oak decline (mortality ca. 2003); these gaps were characterized by standing dead trees with sloughing bark. Our goal was to select only gaps that had two or more dead trees to avoid small, single-tree gaps. However, we did select two gaps that were formed by the death of a single large (>55 cm DBH) white oak. The number of gaps per stand ranged from six to 12 (Table 1). Several gaps (eight in burned stands, four in unburned stands) also contained one or two dead trees other than white oak, but these trees also appeared to have died recently (within the last 10 years). All but two of the 14 dead trees that were not white oaks were still standing with some bark intact. None of the gaps were located in the permanent plots that were established in 1995 (or 2000 for the unburned stand in the Fire and Fire Surrogates study) prior to the initiation of the prescribed fire treatments. Thus, there is no direct predisturbance vegetation data for the 52 gaps. The great majority of gaps occurred on mid- and lower-slope positions on a variety of aspects. A GIS-derived integrated moisture index (IMI) (Iverson et al. 1997) was used to characterize the long-term soil moisture status of the gaps based on landscape position. The IMI is a relative index scaled from 0 (driest) to 100 (wettest).

Field data collection

All data in the gaps were collected in summer 2008. First, we visually estimated and marked the geographic center of each gap. We also flagged the perimeter of the gap based on the canopy dripline of living overstory trees. We measured the length (distance along the hillslope contour) and width (distance perpendicular to the hillslope contour) of each gap through the center point to the perimeter and estimated gap area with $\pi(\text{length} \times \text{width}/4)$ (Hix and Helfrich 2003). We recorded the species and DBH of each standing dead tree ≥10 cm DBH within the gaps. We used an increment borer to collect tree cores at DBH height from at least two understory trees in each gap to estimate the year of gap formation by observed growth releases. All saplings and pole-sized trees, here defined as 3–20 cm DBH, were recorded by species in two size classes (saplings, 3.0–9.9 cm DBH; poles, 10–20 cm DBH) within the perimeter of each gap.

Along the length and width axes of each gap, we established a total of four 10 m^2 (5 m × 2 m) subplots to record advance regeneration. Each subplot was centered along an axis halfway between the center point of the gap and the perimeter. Within each subplot, we recorded the abundance of advance regeneration by species in three size classes: 30–59.9 cm height, 60.0–139.9 cm height, and 140 cm height to 2.9 cm DBH.

Photosynthetically active radiation (PAR) was measured in each gap in August 2008 with a Decagon AccuPAR LP-80 ceptometer. From the center of each 10 m^2 regeneration subplot, a PAR measurement was taken in each of the four cardinal directions at 1 m height.

A second ceptometer was placed in a nearby clearing to record PAR in full sunlight so that the PAR measured in gaps could be expressed as the percentage of full sunlight.

Data analysis

Nested generalized linear mixed models were used to test for significant differences between burned and unburned gaps for the following variables: IMI, gap area, number of dead trees per gap, DBH of dead trees, sapling and pole density, and percentage of full sunlight (SAS 9.2, PROC GLIMMIX; SAS Institute Inc., Cary, North Carolina). The same model was used to test for differences in the abundance of advance regeneration for major species/groups (oaks, hickories, sassafras, shade-tolerant species, other species), the total abundance of all stems, and the relative abundance of oak plus hickory. We combine oaks and hickories in several analyses because they share many ecological traits (e.g., root-centered growth, drought tolerance, intermediate shade tolerance, hard mast production). Shade-tolerance classification is based on Burns and Honkala (1990); however, we classify white ash as shade tolerant rather than intolerant due to its higher degree of shade tolerance when in the seedling stage (noted in Burns and Honkala 1990). Stand, a random effect, was nested within burn treatment, the fixed effect. Thus, in the models, stand was the experimental unit and the gaps within each stand were the sampling units. The variables gap area, number of dead trees per gap, DBH of dead trees, and IMI were normally distributed. The variables sapling and pole density, percentage of full sunlight, and all species/group abundances were skewed to the right and analyzed with the gamma distribution. Because two species/groups (sassafras and other species) had zero abundance in a relatively high number of gaps (sassafras = 48%, other species = 31%), we used the same nested model to first test for significant differences in presence between burned and unburned gaps by specifying the binomial distribution. Then, for only those gaps in which sassafras and other species were present, we applied the nested model with gamma distribution on their abundance. Simple linear regression was used to model the relationship between IMI and gap area (independent variables) and the abundance of larger (60 cm height to 2.9 cm DBH) oak plus hickory stems within both unburned and burned gaps (SAS Enterprise Guide 4; SAS Institute Inc., Cary, North Carolina). Multiple linear regression was used to model the combined effect of IMI and gap area on the abundance of larger oak plus hickory regeneration.

Results

Attributes of gaps

The great majority of gap-forming trees (≥10 cm DBH) were white oaks (204 trees). There were 14 additional trees

Table 3. Mean density of saplings and poles (stems 3.0–20 cm DBH) by species/group in unburned and burned gaps, 2008.

Species/group	Mean density of saplings and poles/ha (SE)	
	Unburned gaps (n = 24)	Burned gaps (n = 28)
American beech (*Fagus grandifolia*)	305.6 (51.2)	20.0 (15.6)
Red maple (*Acer rubrum*)	275.6 (41.2)	40.4 (12.8)
Other shade-tolerant species[a]	130.4 (43.2)	18.8 (9.6)
Sugar maple (*Acer saccharum*)	125.6 (55.2)	8.0 (3.2)
Blackgum (*Nyssa sylvatica*)	101.6 (22.0)	23.6 (8.0)
Hickories (*Carya* spp.)	46.8 (16.4)	30.8 (8.0)
Other shade-intolerant species[b]	10.0 (5.2)	1.6 (1.6)
Oaks (*Quercus* spp.)	2.0 (2.0)	12.4 (4.0)
Total, all species	996 (64.0)	156 (36.0)

[a]In descending order of abundance: blackhaw (*Viburnum prunifolium*), musclewood (*Carpinus caroliniana*), white ash (*Fraxinus americana*), yellow buckeye (*Aesculus flava*), flowering dogwood (*Cornus florida*), downy serviceberry (*Amelanchier arborea*), sourwood (*Oxydendrum aboreum*), American basswood (*Tilia americana*), slippery elm (*Ulmus rubra*), and pawpaw (*Asimina triloba*).

[b]American chestnut (*Castanea dentata*), yellow-poplar (*Liriodendron tulipifera*), and sassafras (*Sassafras albidum*).

that contributed to gap formation comprised of the following species: chestnut oak, black oak, scarlet oak (*Quercus coccinea* Muenchh.), red maple, hickory, and American beech. Because of the deterioration of sapwood in dead trees, the exact year of death could not be determined. Analyses of increment cores collected from surviving subcanopy trees in each gap showed abrupt increases in ring width beginning in 2003 in many trees, suggesting that gaps formed primarily from 2002 to 2003.

The attributes of unburned and burned gaps were similar with respect to soil moisture status, gap area, and the number and size of gap-forming trees (Fig. 1). The IMI of unburned gaps, 47.5 ± 2.3 (least squares (LS) mean ± SE), was not significantly different ($F_{[1,4]}$ = 0.27, p = 0.630) from that of burned gaps (LS mean = 45.9 ± 2.2). The area of burned gaps (LS mean = 259 ± 22.4 m^2) was higher but not significantly different ($F_{[1,4]}$ = 1.91, p = 0.239) from that of unburned gaps (LS mean = 214 ± 23.5 m^2). The number of dead trees in burned gaps (LS mean = 4.6 ± 0.3) was not different ($F_{[1,4]}$ = 3.26, p = 0.145) from that in unburned gaps (LS mean = 3.9 ± 0.3), and the DBH of dead trees was very similar in unburned (LS mean = 43.8 ± 3.2 cm) and burned (LS mean = 41.2 ± 3.1 cm) gaps ($F_{[1,4]}$ = 0.34, p = 0.591).

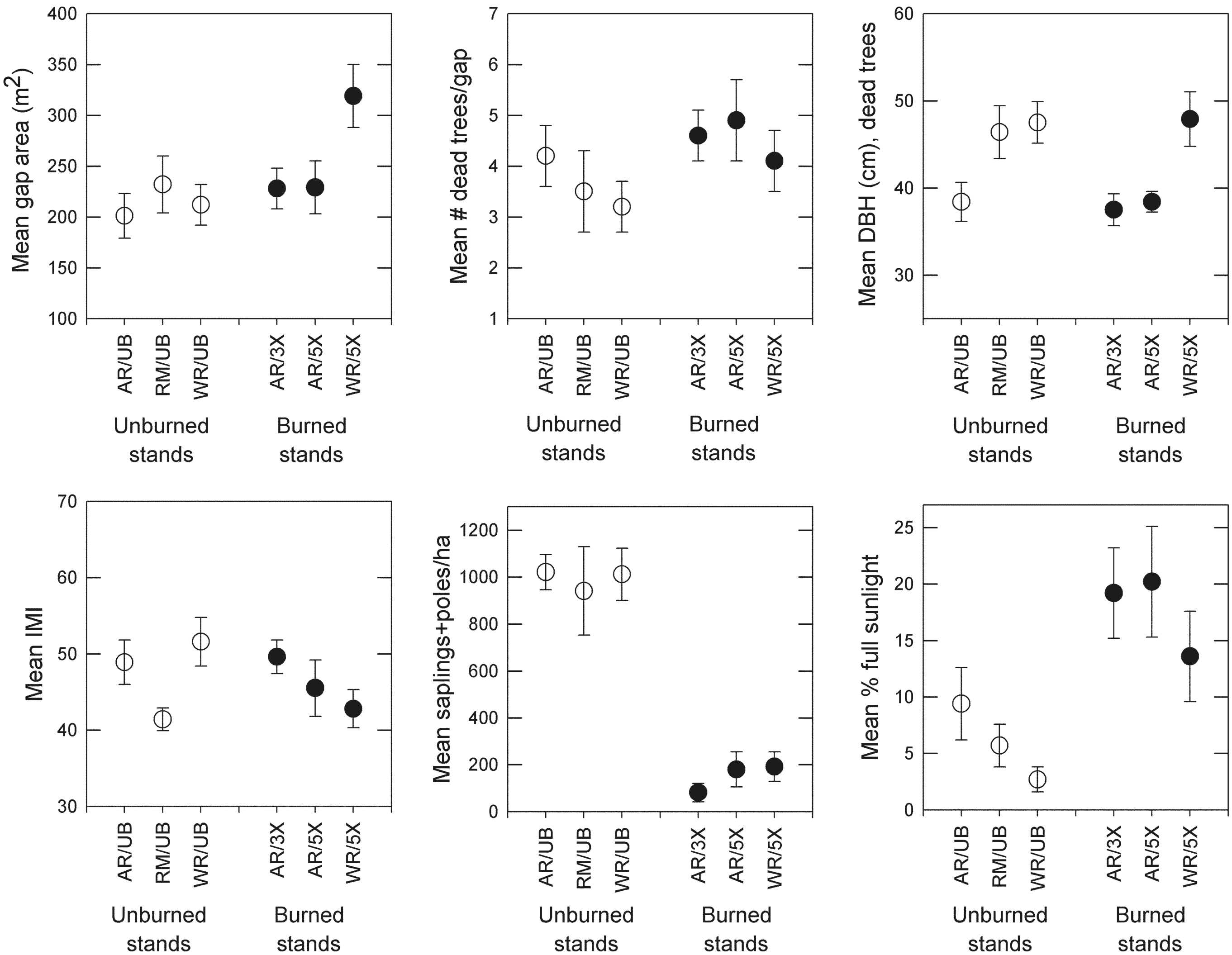
Although burned and unburned gaps were similar in many attributes, understory stem density and light availability were quite different (Fig. 1). The density of saplings and poles (stems 3–20 cm DBH) was significantly greater ($F_{[1,4]}$ = 49.1, p = 0.002) in unburned gaps (LS mean = 999 ± 194 stems/ha) than in burned gaps (LS mean = 156 ± 28 stems/ha). All unburned gaps had more than 500 saplings and poles/ha, 94% of which were shade-tolerant species. American beech, red maple, sugar maple, and blackgum were the most abundant species in the sapling/pole strata of unburned gaps (Table 3). By contrast, only a single burned gap had >500 saplings and poles/ha and one fourth of the burned gaps had no stems in the sapling/pole size class. The percentage of full sunlight was significantly greater ($F_{[1,4]}$ = 10.3, p = 0.033) in burned gaps (LS mean = 18.7% ± 3.7%) than in unburned gaps (LS mean = 7.3% ± 1.6%).

Advance regeneration in burned and unburned gaps

The composition and abundance of advance regeneration (stems 30 cm tall to 2.9 cm DBH) in burned gaps were distinct from those in unburned gaps (Fig. 2). The total density of advance regeneration (all species combined) was significantly greater ($F_{[1,4]}$ = 11.2, p = 0.029) in burned gaps (LS mean = 21 583 ± 3871 stems/ha) than in unburned gaps (LS mean = 9024 ± 1706 stems/ha). The larger stems in the advance regeneration layer, up to 2.9 cm DBH, were typically 2–3 m height. The density of oaks was more than three times greater ($F_{[1,4]}$ = 9.7, p = 0.036) in burned gaps (9066 ± 2568 stems/ha) than in unburned gaps (2523 ± 752 stems/ha). Seventy-one percent of burned gaps had ≥6000 oaks/ha compared to only 17% of unburned gaps. White oak was the most abundant oak in both unburned gaps (57% of all oaks) and burned gaps (67% of all oaks) (Appendix A). The density of white oak in burned gaps (LS mean = 5991 ± 2856 stems/ha) was more than that in unburned gaps (LS mean = 1042 ± 509 stems/ha), but due to high variability, that difference only approached statistical significance ($F_{[1,4]}$ = 6.2, p = 0.062). Black oak was the second most abundant oak and its density was significantly greater ($F_{[1,4]}$ = 6.2, p = 0.062) in burned gaps (LS mean = 1563 ± 347 stems/ha) than in unburned gaps (LS mean = 428 ± 103 stems/ha). Hickories were less abundant than the oaks overall, and although their mean density in burned gaps (LS mean = 1987 ± 477 stems/ha) was more than twice that in unburned gaps (LS mean = 891 ± 231 stems/ha), the difference was not statistically significant ($F_{[1,4]}$ = 5.14, p = 0.086).

Among the other three species/groups, sassafras, when present, was much more abundant in burned gaps than in unburned gaps, while the abundances of shade-tolerant species and other species were similar in burned and unburned gaps (Fig. 2). Sassafras stems ≥30 cm tall were absent from nearly one half of all gaps and it was present in a significantly higher proportion ($F_{[1,4]}$ = 8.64, p = 0.042) of burned gaps (0.71 ± 0.09) than in unburned gaps (0.29 ± 0.09). In gaps where sassafras was present (n = 27), it was much more abundant ($F_{[1,4]}$ = 55.8, p = 0.002) in burned gaps (LS

Fig. 1. Mean values (±SE) for six attributes of canopy gaps in three unburned and three burned stands approximately 5 years after gap formation.

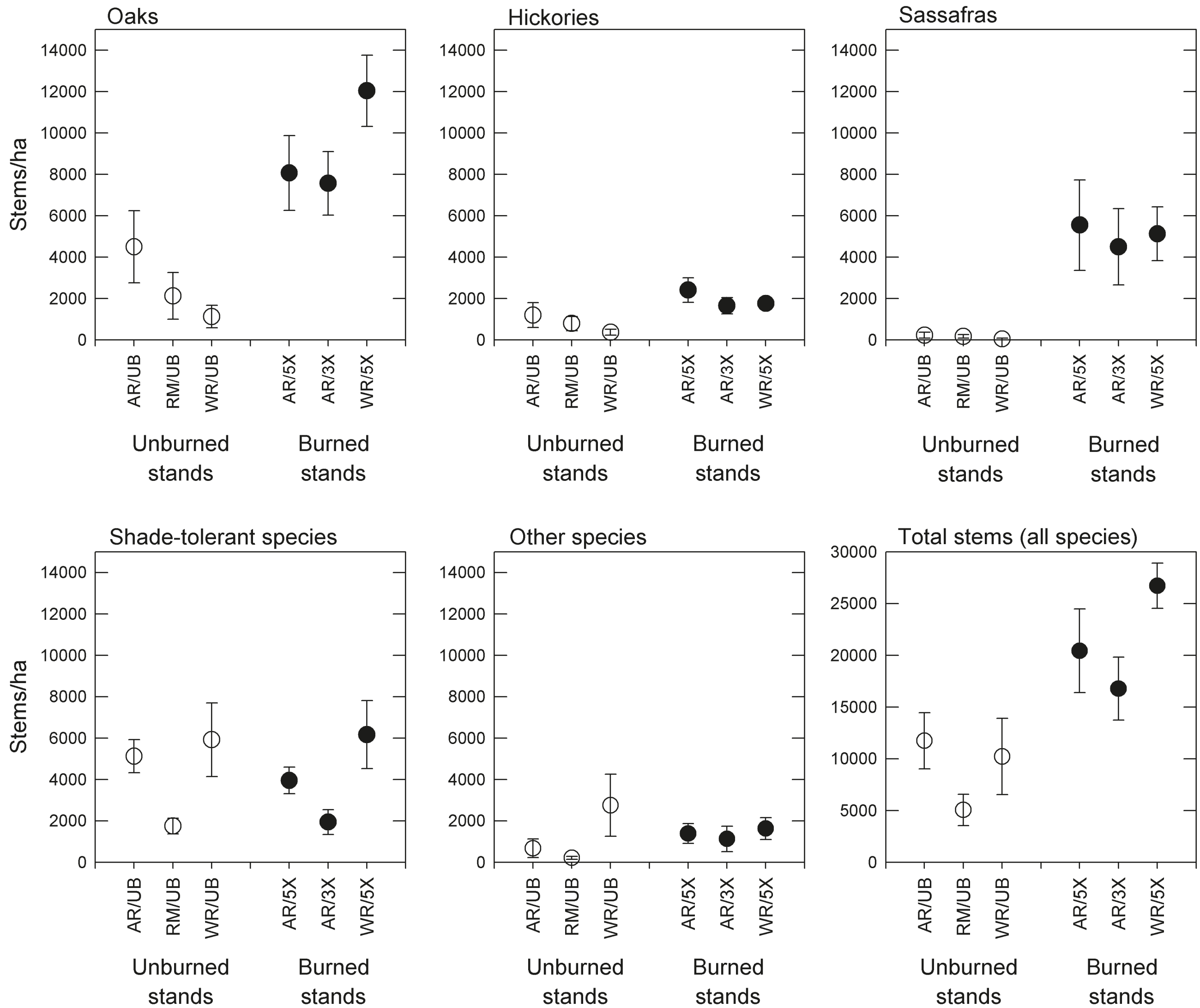


mean = 7156 ± 1233 stems/ha) than in unburned gaps (LS mean = 571 ± 166 stems/ha). The abundance of shade-tolerant species was not significantly different ($F_{[1,4]} = 0.07$, $p = 0.810$) in unburned gaps (LS mean = 3839 ± 1161 stems/ha) and burned gaps (LS mean = 4281 ± 1261 stems/ha). Several individual shade-tolerant species, while not analyzed statistically, exhibited much different abundances in burned and unburned gaps (Appendix A). Among the more common shade-tolerant species, white ash and American hornbeam (*Carpinus caroliniana* Walt.) had higher mean abundances in unburned gaps, while red maple density was higher in burned gaps (Appendix A). The other species group, comprised of shade-intolerant species other than oaks, hickories, and sassafras, was the least abundant of the five species/groups. This group was present in only two thirds of all gaps; both the occurrence ($F_{[1,4]} = 2.42$, $p = 0.195$) and density when present ($F_{[1,4]} = 0.01$, $p = 0.828$) were not significantly different in burned and unburned gaps. The most common species in this group was yellow-poplar, which occurred at a mean density of 969 stems/ha in unburned gaps and 830 stems/ha in burned gaps (Appendix A).

Despite the high density of sassafras in many of the burned gaps, the relative density of oak plus hickory advance regeneration (30 cm tall to 2.9 cm DBH) was significantly greater ($F_{[1,4]} = 8.8$, $p = 0.041$) in burned gaps (LS mean = 52% ± 5.0%) than in unburned gaps (LS mean = 29% ± 6.0%). Oak plus hickory relative density was high (>75%) in only a few ($n = 3$) unburned gaps. Oak plus hickory comprised >30% of stems in only eight of 24 unburned gaps; by contrast, the relative density of oak plus hickory was >30% in nearly all (24 of 28) burned gaps.

The abundance of smaller (stems 30–59.9 cm height) oak plus hickory advance regeneration was not significantly different ($F_{[1,4]} = 0.45$, $p = 0.537$) in unburned gaps (LS mean = 3729 ± 743 stems/ha) and burned gaps (LS mean = 4435 ± 722 stems/ha) (Fig. 3). However, larger oak plus hickory stems (60 cm tall to 2.9 cm DBH) were significantly more abundant ($F_{[1,4]} = 14.8$, $p = 0.018$) in burned gaps (LS mean = 6529 ± 2500 stems/ha) than in unburned gaps (LS mean = 785 ± 311 stems/ha). While 18 of 28 burned gaps had more than 5000 large oak plus hickory stems/ha, only a single unburned gap had a similar density.

Fig. 2. Mean abundance (±SE) of advance regeneration (stems 30 cm tall to 2.9 cm DBH) for major species/groups in canopy gaps within three unburned and three burned stands approximately 5 years after gap formation.



Large oak plus hickory advance regeneration related to gap attributes

Regression analysis of burned gaps showed that the abundance of large oak plus hickory regeneration (60 cm tall to 2.9 cm DBH) was significantly related to topographic soil moisture (IMI) and gap area (Fig. 4). Large oak plus hickory regeneration increased as IMI decreased ($r^2 = 0.31$) and as gaps became larger ($r^2 = 0.34$). Multiple regression analysis indicated that IMI and gap area together were reasonably good predictors of large oak plus hickory density in burned gaps ($r^2 = 0.52$), with the greatest densities of large oak plus hickory occurring in the drier, larger gaps. In unburned gaps, where large oak plus hickory occurred at low densities in nearly all gaps, IMI ($r^2 = 0.03$, $p = 0.445$) and gap area ($r^2 = 0.003$, $p = 0.814$) were not significant predictors of oak plus hickory abundance.

Each of the 19 gaps with the greatest abundance of large oak plus hickory (>5000 stems/ha) also had relatively low densities of saplings and poles (<600 stems/ha); all but one of these gaps were in burned stands (Fig. 5). However, due to the relatively narrow range of sapling/pole densities in the burned gaps, there was not a significant linear relationship between sapling/pole density and the abundance of large oak plus hickory regeneration in burned gaps. A few unburned gaps ($n = 3$), despite high densities of saplings and poles (>1200 stems/ha), also had moderately high densities of large oak plus hickory regeneration (2500–5000 stems/ha).

Understory light levels, measured approximately 5 years after gap formation, were much more variable in burned gaps than in unburned gaps (Fig. 5). In unburned gaps, light levels were <10% of full sunlight in nearly all gaps due to shading from saplings and poles. In burned gaps, understory light was highly variable, exhibiting a continuous range of values from 1% to 50%. There was not a significant linear relationship between percentage of full sunlight and the abundance of large oak plus hickory regeneration.

Discussion

Prior to the initiation of prescribed fire treatments or the formation of gaps, shade-tolerant saplings were abundant in

Fig. 3. Mean abundance (±SE) of (*a*) small (30–59.9 cm tall) and (*b*) large (60 cm tall to 2.9 cm DBH) oak plus hickory advance regeneration in canopy gaps within three unburned and three burned stands 5 years after gap formation.

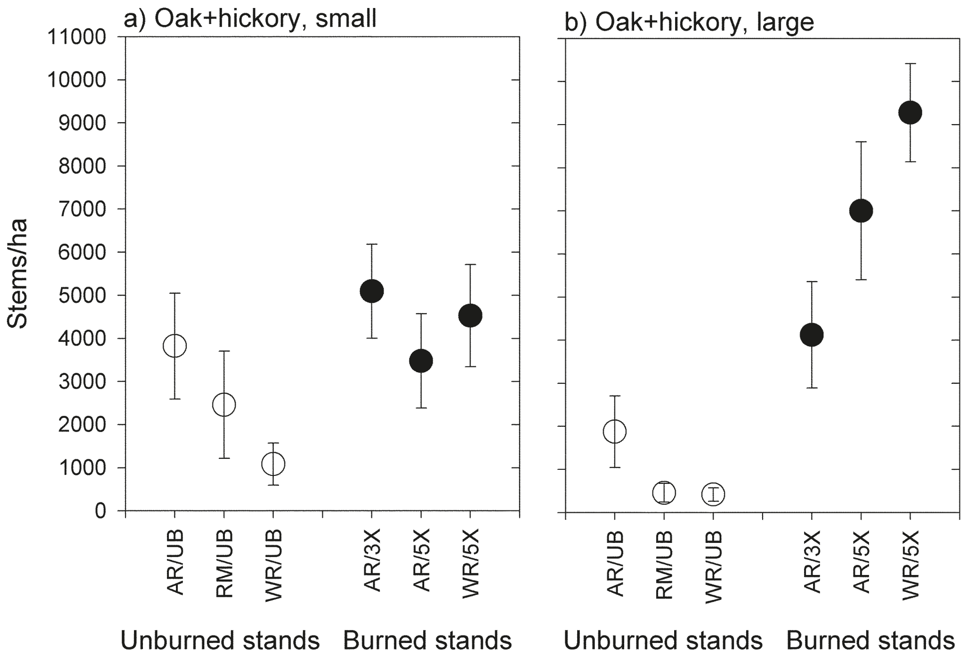
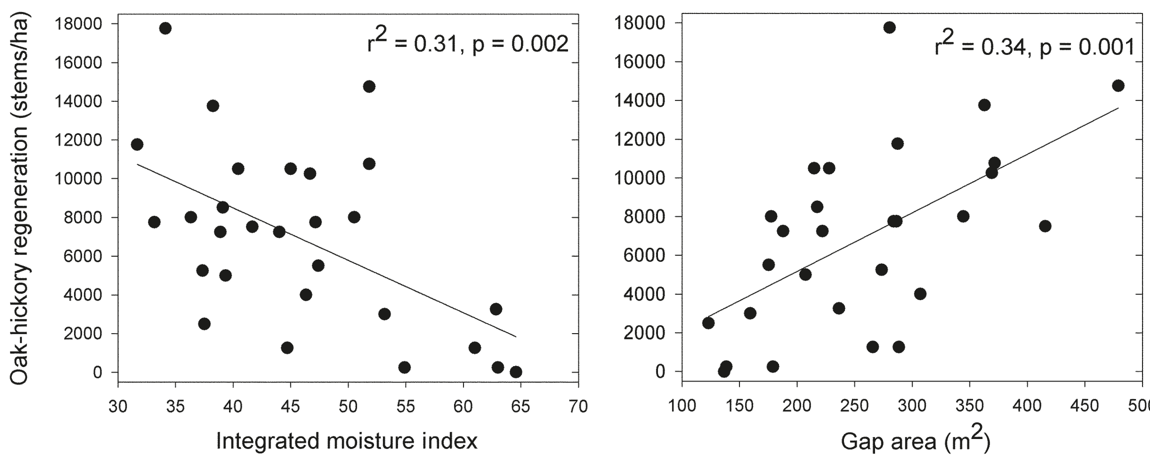


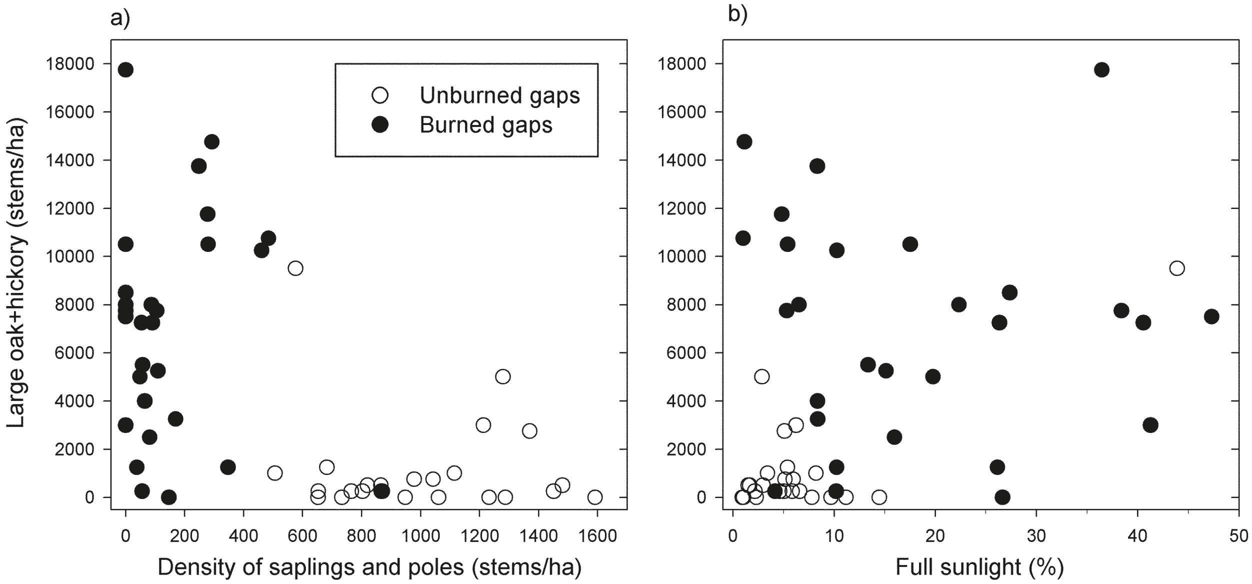
Fig. 4. Linear regression analysis of burned gaps with the abundance of large oak plus hickory advance regeneration (60 cm tall to 2.9 cm DBH) as the dependent variable and the integrated moisture index and gap area as independent variables.



the fully stocked oak stands that comprised this study, while oak plus hickory seedlings were moderately abundant but small in stature. In canopy gaps that formed within stands that had been burned repeatedly, large oak plus hickory regeneration (stems ≥60 cm tall) was much more abundant than in similar gaps located in unburned stands. The burned gaps had much lower densities of shade-tolerant saplings and poles and also higher levels of understory light. These findings suggest that the greater light levels attained in the burned gaps facilitated the development of larger oak plus hickory stems. In sharp contrast, unburned gaps were being filled rapidly by shade-tolerant saplings and poles and thus had lower understory light levels and, correspondingly, lower densities of large oak plus hickory.

In oak-dominated stands, the abundance of larger oak seedlings has been shown to increase with understory light levels, if other factors such as competition or herbivory are not limiting (Carvell and Tryon 1961). Studies that have compared oak seedling growth in different light levels, both in artificial settings and in forests, have shown poor growth, aboveground and belowground, when light levels are <10% of full sun (Gottschalk 1985; Crow 1992; Brose 2008; Rebbeck et al. 2011); these studies have also shown increased survival and (or) growth of oak seedlings with increasing light availability. In our study, nearly all unburned gaps had <10% of full sunlight, 5 years after gap formation, due to gap filling by shade-tolerant saplings and poles. In contrast, understory light levels were greater in the burned gaps, averaging 19% of full sunlight. However, the abundance of large oak plus hickory was not strongly correlated with percentage of full sunlight in burned gaps; this was likely due, at least in part, to the fact that the advance regen-

Fig. 5. Scatterplots of the abundance of large oak plus hickory advance regeneration (stems 60 cm tall to 2.9 cm DBH) and (*a*) the density of saplings and poles (3–20 cm DBH) and (*b*) the percentage of full sunlight in burned and unburned gaps.



eration layer had overtopped the PAR sensor (1 m height) in a number of sampling locations.

In permanent plots located in the burned stands, a comparison of oak plus hickory advance regeneration (≥30 cm tall) in 2002, just prior to gap formation (Hutchinson et al. 2005), with that found in the canopy gaps in 2008 suggests relatively rapid height growth of seedlings after gap formation ca. 2003. In 2008, oak plus hickory advance regeneration was six times more abundant and was also larger (62% of stems >60 cm tall) in burned gaps than in the same burned stands just prior to gap formation in 2002 (22% of stems >60 cm tall). Even relatively small increases in light availability in the burned stands prior to gap formation, due to reduced sapling and midstory density (Hutchinson et al. 2005), likely favored the development of greater belowground carbohydrate reserves in the oaks and hickories. These reserves are needed for rapid height growth after a canopy opening (Sander 1971**;** Dillaway et al. 2007). In addition to facilitating the development of larger oak regeneration, repeated burns may have favored the accumulation of oak seedlings (Johnson et al. 2002) by reducing mortality and (or) increasing establishment; however, without direct predisturbance regeneration data in the gap locations, this is only conjecture. Our findings also suggest that improved “oak regeneration potential” (see Johnson et al. 2002) in burned stands may not be apparent until after a canopy disturbance occurs.

Oak regeneration is typically larger and more abundant on drier landscape positions, due to less competition and more light availability (Johnson et al. 2002). Indeed, we found that the abundance of larger oak plus hickory regeneration increased as gaps became drier (lower integrated moisture index) and larger, but only for gaps that had been burned. In the unburned gaps, larger oak plus hickory stems occurred at low densities in nearly all gaps, regardless of IMI or gap size, presumably due to lower light availability. Our findings suggest that the high densities of shade-tolerant saplings and poles that occurred in nearly all unburned gaps was the primary limiting factor to the development of larger oak plus hickory regeneration, even on drier sites.

Shade-tolerant species, which dominated a dense sapling layer prior to the initiation of prescribed fire treatments, continued to dominate the sapling and pole strata in unburned gaps in 2008 but occurred at very low densities in burned gaps. Despite the fact that most shade-tolerant species also respond to canopy gaps with increased growth, advance regeneration of all shade-tolerant species, collectively, was no more abundant in the higher light levels of the burned gaps than in the unburned gaps. This finding suggests that sprouting from shade-tolerant saplings and poles was not as vigorous as has been reported in several other prescribed fire studies. For example, red maple stem density has been shown to increase substantially by vigorous postfire sprouting (Albrecht and McCarthy 2006; Blankenship and Arthur 2006). We hypothesize that a lack of vigorous sprouting by red maple and other shade-tolerant species in our burned stands resulted from repeated topkilling in relatively low-light conditions prior to gap formation (Hutchinson et al. 2005).

Similar to the oaks and hickories, sassafras was larger and more abundant in burned gaps than in unburned gaps. Although rated as shade intolerant, sassafras can persist in the understory of mixed-oak forests (Burns and Honkala 1990). After fire, sassafras has been shown to have high rates of survival by resprouting and increased height growth and it also attains higher densities primarily by root suckering (Dey and Hartman 2005; Albrecht and McCarthy 2006; Alexander et al. 2008). In our study, 5 years after gap formation, sassafras was a strong competitor for growing space in many of the burned gaps but not in unburned gaps. It is unclear whether the shade-intolerant sassafras will ultimately be able to compete in these moderate-sized gaps with the more tolerant oaks and hickories, which also likely have greater belowground carbohydrate reserves from which to draw. In our study area, sassafras is uncommon in the overstory of today’s forests, even though fire occurred frequently prior to the suppression era (Hutchinson et al. 2008). This suggests that, despite its current abundance in the burned gaps, sassafras may not be a strong competitor as stand development proceeds.

Although white oak remains the most widespread and abundant oak in the eastern United States (Iverson et al. 1999), its dominance declined in many areas with the clearance and industrial exploitation of forests from the mid-1800s to the early 1900s, a phenomenon that is continuing in the present (Abrams 2003). In our study, white oak was the most abundant oak in the advance regeneration layer of burned gaps. On the one hand, this is not surprising, given that we studied patches where white oak was dominant in the overstory; however, the successful regeneration of white oak is often more difficult than that of other upland oaks, particularly in even-aged management systems, due to its slow juvenile growth rates (Brose 2008; Rebbeck et al. 2011). Of the five common upland oaks in our region, white oak is the most shade tolerant (Burns and Honkala 1990), and our findings suggest that white oak seedlings were able to persist in the burned stands prior to gap formation, despite relatively low-light conditions, and then exhibited significant height growth after gap formation.

Oak advance regeneration requires an adequate release to ascend to the canopy, which is typically executed with even-aged silvicultural methods that create large openings (Loftis 2004). However, if oak seedlings are large and competition is limited, oaks can ascend to the canopy in smaller openings like those in our study (Lorimer 1983). In the burned stands, oaks and hickories appear to be well positioned to fill many of the canopy gaps, given the abundance of large oak plus hickory stems and the low densities of shade-tolerant saplings and poles. Rentch et al. (2003) reconstructed disturbance histories of several old-growth oak forests dominated by white oak and found that, historically, oaks originated and ascended to the canopy in both large openings and smaller gaps, similar to the those formed in our study. The authors hypothesized that understory light levels were higher in the past, due at least in part to periodic fires, which allowed the relatively shade-tolerant white oak to persist and eventually ascend to the canopy in small as well as large openings.

Management implications

In eastern oak ecosystems, the use of prescribed fire has increased substantially in the last 20 years, almost exclusively on public lands. Results of this study indicate that land managers may improve the regeneration potential of oak and hickory in mature stands with repeated low-intensity prescribed fires. However, this strategy will take considerable time and the benefits to oak and hickory regeneration may not be realized until after a canopy disturbance. For oak forests located on public lands, prescribed fire may be the “tool of choice” for land managers seeking to sustain oak and hickory. It is cost-effective, particularly when larger acreages can be burned with aerial ignition. In addition to its applications for improving oak regeneration, prescribed fire has other ecological effects that may be desirable. In stands where no timber harvesting is planned in the foreseeable future (e.g., 20 years), repeated burns can be applied to gradually improve the vigor and competitiveness of oak and hickory regeneration in advance of natural canopy disturbances (e.g, windthrow, ice damage, insects, disease). In stands where timber harvesting is planned, and prescribed fire is the desired tool to improve oak regeneration, our results suggest that multiple burns should be initiated well in advance (~10 years) of the harvest.

In this study, repeated prescribed fires favored the development of large oak and hickory advance regeneration after a canopy disturbance. Because our study occurred after a cycle of three or five burns, it is unclear whether one or two fires would have promoted oak and hickory regeneration in gaps. However, the consensus is that a single fire does not improve the competitive status of oak regeneration (Brose et al. 2006). Also, oak forests with different characteristics than those in this study may not respond to repeated burns in a similar manner. In our stands, prior to treatments, oaks and hickories were highly dominant in the overstory and seedlings were moderately abundant although small. In forests where oak and hickory regeneration is more sparse, multiple burns will only have a positive effect if germination and establishment from seed are enhanced by burning (Barnes and Van Lear 1998; Royse et al. 2010). Also, in our study, multiple fires reduced sapling and pole densities substantially, but in forests where the midstory stratum consists of larger trees that are more fire resistant, fire alone will likely be ineffective at reducing stand density and increasing light to the forest floor. Where this is the case, herbicide treatments of larger midstory trees could supplement the ability of prescribed fires to reduce the density of saplings and smaller midstory trees.

We found that larger white oak regeneration was abundant in moderate-sized canopy gaps (200–400 m^2) that had been burned repeatedly prior to gap formation. Although uneven-aged management is not typically used in oak forests (Johnson et al. 2002; Loftis 2004; Brose et al. 2008), our results suggest that for white oak, the most shade tolerant of the upland oaks, the use of repeated burns prior to the creation of moderate-size canopy openings may be a feasible regeneration strategy. Periodic fires coupled with natural canopy openings of various sizes are thought to have sustained the presettlement-era dominance of white oak across much of the eastern United States (Abrams 2003).

Acknowledgements

We thank William Borovicka and Levi Miller for leading the field data collection; Richard Craig, Timothy Fox, Matthew Peters, Zachary Moor, and Jonathan Schaeffer provided field assistance. We thank Joan Jolliff and Timothy Fox for entering the data. We thank Patrick Brose, John Kabrick, and two anonymous reviewers for many helpful suggestions on a previous draft. We thank John Stanovick and Alejandro Royo for statistical consultation. We thank our land management partner, the Ohio Division of Forestry, owner of the Vinton Furnace State Experimental Forest. The original funding for the prescribed fire study and the Fire and Fire Surrogates study was provided by the Washington Office of the USDA Forest Service and the Joint Fire Science Program, respectively. Additional support for this study was provided by the Northern Research Station, USDA Forest Service.

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Appendix A

Table A1. Mean abundance of advance regeneration (stems 30 cm tall to 2.9 cm DBH) in unburned and burned gaps.

			Mean abundance (stems/ha (±1 SE))	
Species	Common name	Species/group	Unburned gaps (n = 24)	Burned gaps (n = 28)
Acer rubrum	Red maple	Shade tolerant	891 (291)	2196 (610)
Amelanchier arborea	Downy serviceberry	Shade tolerant	63 (35)	277 (112)
Carpinus caroliniana	Musclewood	Shade tolerant	843 (231)	278 (155)
Carya spp.[a]	Hickories	Hickory	891 (312)	1987 (262)
Cornus florida	Flowering dogwood	Shade tolerant	219 (71)	375 (82)
Fagus grandifolia	American beech	Shade tolerant	385 (98)	201 (63)
Fraxinus americana	White ash	Shade tolerant	1333 (302)	205 (63)
Liriodendron tulipifera	Yellow-poplar	Other	969 (430)	830 (254)
Nyssa sylvatica	Blackgum	Shade tolerant	427 (174)	281 (94)
Oxydendrum arboretum	Sourwood	Shade tolerant	104 (33)	304 (130)
Quercus alba	White oak	Oak	1745 (586)	6143 (956)
Quercus coccinea	Scarlet oak	Oak	302 (95)	505 (160)
Quercus prinus	Chestnut oak	Oak	281 (260)	670 (207)
Quercus rubra	Red oak	Oak	307 (75)	321 (76)
Quercus velutina	Black oak	Oak	427 (123)	1563 (276)
Sassafras albidum	Sassafras	Sassafras	167 (73)	5112 (1056)
Uncommon species[b]		Shade tolerant/other	323 (117)	683 (194)

[a]Hickories were predominantly *Carya glabra* (pignut hickory) and *Carya tomentosa* (mockernut hickory). *Carya cordiformis* (bitternut hickory) was also present.

[b]Uncommon species (ST, shade tolerant; O, other, intolerant): sugar maple (*Acer saccharum*) (ST), yellow buckeye (*Aesculus flava*) (ST), pawpaw (*Asimina triloba*) (ST), American chestnut (*Castanea dentata*) (O), redbud (*Cercis canadensis*) (ST), hawthorn (*Crataegus* spp.) (O), persimmon (*Diospyros virginiana*) (O), black walnut (*Juglans nigra*) (O), bigtooth aspen (*Populus grandidentata*) (O), black cherry (*Prunus serotina*) (O), American basswood (*Tilia Americana*) (ST), and blackhaw (*Viburnum prunifolium*) (ST).