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Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture

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Citation: Iverson, L. R., T. F. Hutchinson, M. P. Peters, and D. A. Yaussy. 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. Ecosphere 8(1):e01642. 10.1002/ecs2.1642

Abstract. By tracking oak-hickory (*Quercus-Carya*) regeneration for 13 yr across management-manipulated light and topographically driven moisture gradients after partial harvest and three prescribed fires, we document best-case conditions to promote advanced oak regeneration, and thereby provide a promising management tool to reverse the downward spiral in oak that plagues much of the Central Hardwoods within the eastern United States. This study was established in 2000 to assess regeneration following prescribed fire (spring of 2001, 2005, and 2010) in combination with partial harvest (late 2000) across two sites in southern Ohio. Each of the four 20+ ha treatment units (two partial harvest and burn, two controls) were modeled and mapped for long-term moisture regime using the Integrated Moisture Index (IMI) , and a 50-m grid of sampling points established throughout the units. Vegetation and light were sampled at each gridpoint before and after treatments, in 2000, 2001, 2004, 2006, 2009, and 2013. The partial harvest and burn treatments generally had more light which resulted in an increased number of oak stems. The fires promoted heterogeneity (pyrodiversity) in tree mortality and light availability, and consequently oak-hickory regeneration, mostly following IMI patterns with the drier portions of the landscape having more fire, more light penetration, and greater regeneration compared to moist locations. Several other species also had marked variations in numbers and size throughout this period, depending on landscape variation in fire intensity and moisture regimes. These included *Acer rubrum* and *Liriodendron tulipifera* which expanded initially then collapsed after repeated fire, and *Sassafras albidum* which continued to flourish on dry sites. Based on this study, we recommend for topographically appropriate dry and intermediate sites, a partial harvest followed by two or three dormant-season fires (depending on fire intensity) allowing roughly 6–18% light to penetrate the forest floor. This will promote oak-hickory into the advanced oak regeneration status. Then, following a hiatus from burning for some years to further advance oak-hickory growth without topkill, some proportion of oaks and hickories can be expected to advance to the canopy following natural disturbance or harvest of current canopy. On mesic sites, though treatments demonstrated here do improve oak-hickory regeneration, the relative cost to benefit would be high.

Key words: canopy openness; Central Hardwoods region; hickory (*Carya*); Integrated Moisture Index; maple (*Acer*); moisture regime; oak (*Quercus*); oak advanced regeneration; oak regeneration; Ohio; partial harvest; prescribed fire; topographic influences.

Received 21 September 2016; revised 15 November 2016; accepted 15 November 2016. Corresponding Editor: Debra P. C. Peters.

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Introduction

A large portion of the Central Hardwoods forests, including most of those in Ohio, are undergoing a conversion from dominance by oak-hickory (*Quercus* and *Carya*) to maple (*Acer*) and other shade-tolerant and/or mesophytic species (Abrams 2003, Fei et al. 2011). This is often referred to as "mesophication" (Nowacki and Abrams 2008) and is attributed to multiple interacting factors (McEwan et al. 2011). U.S. Forest Service forest inventories conducted in Ohio during 1968, 1991, 2006, and 2011 (Kingsley and Mayer 1970, Dennis and Birch 1981, Griffith et al. 1993, Widmann et al. 2009, 2014) indicated that the proportion of total volume in oak and hickory has declined substantially relative to red and sugar maple (*A. rubrum, A. saccharum*), yellow-poplar (*Liriodendron tulipifera*), and black cherry (*Prunus serotina*). The U.S. Forest Inventory and Analysis units have documented this trend throughout the region (Fei et al. 2011).

Across much of the Central Hardwoods, mature closed-canopied forests are usually characterized by an oak-dominated canopy (even in mesic landscape positions) and small oak seedlings that are often relatively abundant, at least on drier sites. However, larger oak seedlings and saplings are typically sparse (Johnson et al. 2009, Arthur et al. 2012). Though oak regeneration has been an object of study for many decades (Carvell and Tryon 1961, Brose et al. 2014), this trend continues to prompt large scientific efforts to assess the problem and search for management solutions (e.g., Loftis and McGee 1993, McShea and Healy 2002, Johnson et al. 2009, Arthur et al. 2015), including a better understanding of the historic role of fire and the use of prescribed fire in oak forests (Hutchinson et al. 2005*a*, 2005*b*, Hutchinson et al. 2008, Brose et al. 2013, Varner et al. 2016).

Several factors contribute to poor oak regeneration in this region. In some regions, herbivory by deer has been shown to greatly affect the success of oak regeneration (e.g., in north-central West Virginia, Nuttle et al. 2013). Elsewhere under pervasive closed-canopy conditions, the oaks are outcompeted by more shade-tolerant species like the maples (Loftis and McGee 1993). When light is not limiting and in the absence of fire (e.g., after a clearcut), faster-growing shade-intolerant species such as yellow-poplar often out-compete oak, particularly on higher-quality sites (Beck 1990). Thus, an intermediate level of light appears to be optimum for oak regeneration relative to other species and, in our earlier paper evaluating 7 yr of this experiment, oak regeneration in southern Ohio was most competitive at about 9–19% canopy openness (Iverson et al. 2008). Note also, however, that optimum light levels may vary to some degree among oak and hickory species.

The success of oak regeneration after a canopy-opening disturbance has been shown to vary across a soil moisture gradient, with oak dominating only under relatively xeric conditions (Iverson et al. 1997). Topographic conditions of aspect, position, and curvature on a slope as well as the water-holding capacity of the soil will largely dictate the long-term soil moisture regime, which influences many characteristics of the vegetation. In topographically dissected settings, the moisture regime can change dramatically in a relatively short horizontal distance. The Integrated Moisture Index (IMI) has successfully captured this variation across various landscapes (Iverson and Prasad 2003).

Prior to Euro-American settlement (ca. 1800), oaks were the dominant tree species across most of the Allegheny Plateau of southern Ohio (Beatley and Bartley 1959, Dyer 2001), consistent with their foundational status throughout east-central Unites States (Hanberry and Nowacki 2016). In southern Ohio, dendrochronology studies on trees from the period ca. 1870–1935 have shown that fire occurred frequently (~10 yr fire interval) as forests were regenerating after exploitive timber harvesting in the 1800s (Sutherland 1997, McEwan et al. 2007, Hutchinson et al. 2008). Organized fire suppression was instituted in Ohio in 1923, and by the mid-1930s, the extent of burning had been sharply reduced (Leete 1938). Throughout much of the eastern United States, similar dramatic decreases in fire frequency have contributed to the widespread establishment of maples and other fire-sensitive species that now threaten the sustainability of oak dominance (Nowacki and Abrams 2008). Returning fire to the landscape has had mixed results, in that a meta-analysis of 32 prescribed fire studies revealed that fire alone did not consistently increase the competitive position of oaks, unless fires were conducted during the growing season and several years after a significant reduction in

overstory density (Brose et al. 2013). However, Hutchinson et al. (2012) did find that oak-hickory regeneration competed well in natural canopy gaps that formed in stands with a recent history of frequent dormant-season fires.

In 2000, we initiated a long-term study in southern Ohio to assess the effects of partial harvest (hereafter shortened to "harvest") and repeated prescribed fires as a management tool to improve oak regeneration. The study was implemented as part of the national Fire and Fire Surrogates Study (FFS; Schwilk et al. 2009, McIver et al. 2012), of treatment alternatives to reduce fuels and restore open-structured forest types that were historically sustained by frequent surface fires. Albrecht and McCarthy (2006) evaluated the initial (years 1–4) effects of the partial harvest and single fire on tree regeneration and found that the competitive position of oak regeneration had decreased because of the abundant sprouting and establishment of competitors (e.g., *A. rubrum*, *L. tulipifera*, *Sassafras albidum*). They suggested additional fire was needed to reduce the competition and promote the development of larger oak advance reproduction. The initial promotion of undesirable species was also reported in the North Carolina FFS site, also in mixed-oak forests (Waldrop et al. 2008). As large-scale prescribed fires are becoming more common on public lands in eastern oak ecosystems, particularly in the Appalachian Mountains, it is important to better understand the connections between topography, fire intensity, and vegetation response in a periodic fire regime.

Deer density in this study was ~6 deer/km^2, two to three times lower than the 11–18 deer/km^2 reported for north-central West Virginia in Nuttle et al. (2013). Apsley and McCarthy (2004), working in the FFS sites studied in this paper, found no herbivory effect on species richness and seedling density. They did find, however, a 16% reduction in seedling height due to browsing. Therefore, we did not consider herbivory as a primary factor in our analysis.

A primary objective of this study is to measure the long-term effects of partial harvest and repeated prescribed fire on the light environment, vegetation structure, and tree regeneration, with emphasis on the response of oaks and hickories relative to competing species. We pursue this objective via a landscape-level approach across two sites where we study oak-hickory regeneration response to management across *both* light and moisture gradients, and along a 13-year timeline following initial treatments. We thus concomitantly evaluate the influences of topography, moisture, burn intensity, partial harvest, and competition on regeneration response, all with an intent to enable prediction of oak-hickory regeneration success in the context of landscape variability and management.

Methods

Site description

Our study is located on two sites in Vinton County, Ohio. The Raccoon Ecological Management Area site (REMA; 39°12′41″ N, 82°23′09″ W) is in the Vinton Furnace State Forest, within the Vinton Furnace Experimental Forest. The Zaleski site (ZAL; 39°21′17″ N, 82°22′06″ W) lies within the Zaleski State Forest.

The sites lie within the unglaciated Allegheny Plateau physiographic region, characterized by dissected topography (narrow ridges and valleys) with <100 m of local relief. The uplands consist of mixed-oak forests, which grade into mixed-mesophytic communities in ravines and other sheltered locations (Beatley and Bartley 1959). The current even-aged overstory regenerated ca. 1850–1900 after being extensively harvested for charcoal to fuel nearby iron furnaces (Stout 1933, Iverson et al. 1997).

In the overstory, the most abundant oaks are white (*Quercus alba*), chestnut (*Q. prinus*), and black (*Q. velutina*). Red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), pignut hickory (*Carya glabra*), mockernut hickory (*C. tomentosa*), and yellow-poplar (*Liriodendron tulipifera*) are common associates. In the midstory and sapling strata, red maple (*Acer rubrum*) and other shade-tolerant species, such as blackgum (*Nyssa sylvatica*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*), are dominant in all but the most xeric landscape positions.

Though the two sites are similar in many ecological characteristics including vegetative compositions, there is a fundamental topographical difference between harvest + burn units: The ZAL site is rather concave with gentle, relatively short slopes and with the lowest elevations near the center of the unit. In contrast, the REMA unit is convex with its highest elevations along an

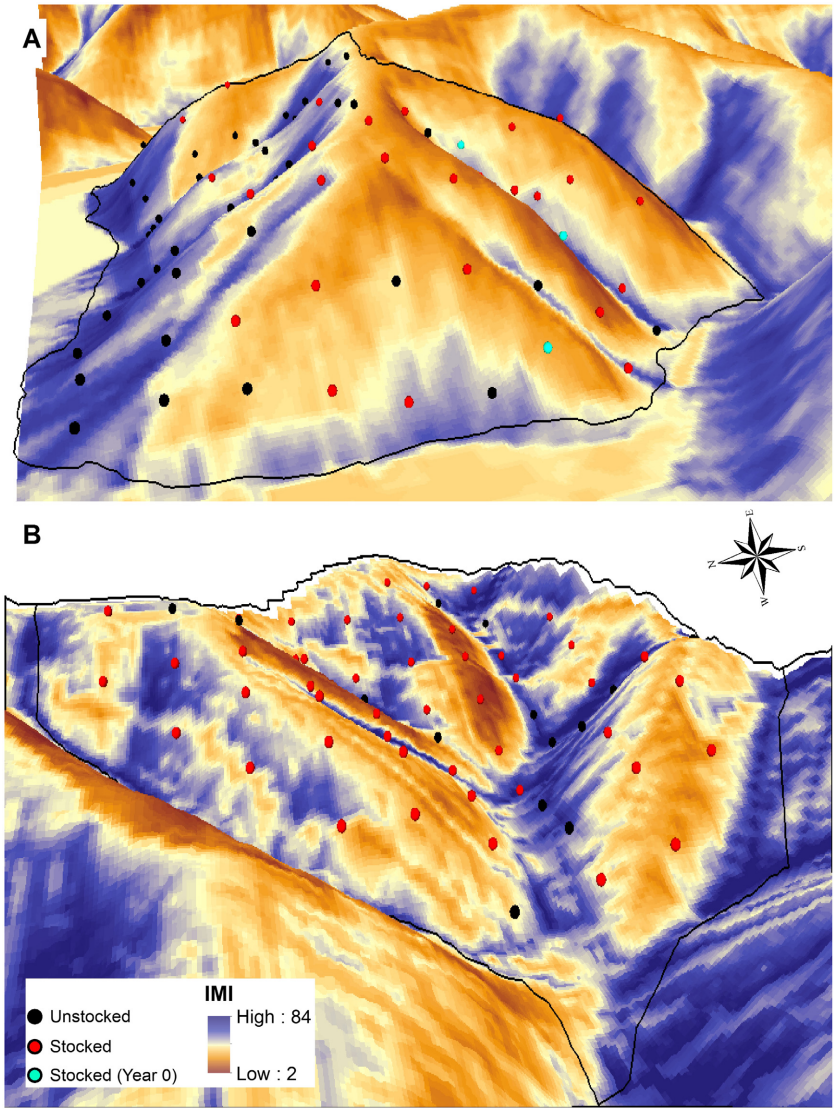

Fig. 1. Three-dimensional perspective on the (A) REMA HB and (B) ZAL HB units. Note the convex topography for REMA and concave topography for ZAL. Also presented is the Integrated Moisture Index (IMI), and the grid-points indicating whether the point was stocked prior to treatment (Y0), after treatment (Y13), or unstocked (see *SILVA:OAK* sections in text). REMA, Raccoon Ecological Management Area; ZAL, Zaleski; HB, harvest and burn unit.

east-west spine at the center, and has longer, steeper slopes (Fig. 1). This topographical contrast had large implications for fire intensity and effects, with much larger and more heterogeneous fire impacts at REMA while at ZAL, conditions were more homogeneous. Thus, a comparative analysis between sites allows us to better characterize oak-hickory regeneration across a wide variation in topographic conditions which represent much of the Central Hardwoods region.

Study design

The FFS study design consists of four treatments on each site, resulting in 12 treatment units of 20–25 ha each. The four treatments are untreated control (C), partial harvest, prescribed burning, and a combination of harvest and burning (HB; Waldrop et al. 2008). For the present study, we restricted sampling to only the C and HB units on two sites (four treatment units), but systematically sampled these units intensively across the dissected

Table 1. Timing, weather, sensor temperatures, and resulting change in % open sky for fires in 2001, 2005, and 2010.

Item	ZAL 2001	REMA 2001	ZAL 2005	REMA 2005	ZAL 2010	REMA 2010
Date	4 April	5 April	5 April	11 April	5 April	14 April
Year of study	1	1	5	5	10	10
Maximum air temperature, °C	19	24	28	28	28	24
Minimum relative humidity, %	23	21	18	13	36	23
Days since rain	2	3	3	4	7	6
Sensor temperature, overall, °C	139	124	211	169	180	249
Sensor temperature, dry IMI, °C	171.8	160.3	214.8	218.0	186.8	328.3
Sensor temperature, intermediate IMI, °C	127.1	156.1	191.2	150.3	188.3	272.8
Sensor temperature, mesic IMI, °C	117.5	94.3	183.3	142.2	112.3	179.9
Change in open sky, overall, %	4.4	6.7	−2.4	−0.4	0.2	7.8
Change in open sky, dry IMI, %	5.1	9.3	−2.6	6.2	0.4	13.8
Change in open sky, intermediate IMI, %	4.3	6.5	−2.1	−1.5	0.0	7.0
Change in open sky, mesic IMI, %	3.3	4.8	−3.4	−5.8	0.2	4.2

Notes: In 2005 and 2010, temperatures and open sky were only recorded for a small proportion of the grid points. IMI, Integrated Moisture Index; REMA, Raccoon Ecological Management Area; ZAL, Zaleski.

landscape. The grid of sampling points (plots) was established every 50 m throughout the units using a global positioning system (GPS). The number of plots sampled per unit was 45 at ZAL C, 60 at ZAL HB, 66 at REMA C, and 71 at REMA HB. These 242 points are the basis of all analyses reported in this paper, although in some analyses, incomplete data reduced the plot numbers to 237.

The IMI was used to capture the influence of varying topography and soils across the landscape (Iverson et al. 1997). The IMI is a GIS model (0–100 scale) of long-term potential moisture availability based on solar radiation, position on the slope, curvature of the landscape, and water-holding capacity of the soils. IMI has been directly related to soil moisture (Iverson et al. 2004*b*) and has been used to predict forest site productivity and composition, understory vegetation, soil nutrients, and bird distributions (Dettmers and Bart 1999, Hutchinson et al. 1999, Boerner 2006, Anning et al. 2013). Here, we categorized plots into one of three IMI classes, earlier generated for generally equal area distribution and for ease in interpretation (Iverson and Prasad 2003): dry, intermediate, and mesic. IMI scores ranged from 8 (very dry) to 84 (very mesic) on REMA HB (average 43.7) and from 14 to 76 on ZAL HB (average 39.5), again indicating the higher level of heterogeneity on the REMA site.

Treatments

Partial harvests occurred from December 2000 to February 2001. Removals were concentrated in the smaller size classes (trees 15–30 cm diameter at breast height [dbh]) and oaks and hickories were favored for retention. The ZAL HB unit had greater stand density than the REMA HB unit and was also harvested more heavily to open the canopy. For the ZAL HB site, stand density (trees >10 cm dbh) was reduced by 35%, from 447 to 292 stems per hectare; basal area was reduced from 26 to 19 m^2/ha (Waldrop et al. 2008). On the REMA HB unit, stand density was reduced 20% from 372 to 297 stems/ha and basal area was reduced from 28 to 23 m^2/ha.

Prescribed fires were conducted three times, all in early April but which resulted in quite widely varying sensor temperatures at 25 cm above ground (Iverson et al. 2004*a*), and change in percent open sky (Table 1). The first fires in 2001 were generally of low intensity with flame lengths <1 m and relatively low sensor temperatures (placed at each gridpoint), resulting in very little overstory tree mortality (Iverson et al. 2003, 2008).

The second and third prescribed fires were conducted in 2005 and 2010 and the relatively drier weather conditions coupled with coarse fuels being cured from the harvesting and prior burns resulted in higher-intensity fires, with flame lengths reaching 1–2 m or greater in some areas and much higher sensor temperatures (placed only on 10 gridpoints per unit—described in Waldrop et al. (2008), Table 1). Fires were generally of low intensity on the north-facing slopes (mesic IMI) but moderate to very high intensity on the southwest-facing slopes (dry IMI), especially the long SW slope of REMA in 2010 where the maximum temperature sensed by any probe was 770°C (Table 1).

Light sampling

To estimate understory light transmission levels, hemispherical photographs were taken at each gridpoint in July of 2000, 2001, 2006, 2009, and July–August 2013 with a digital camera leveled 1.5 m above the forest floor. The images were analyzed for percentage open sky with the Gap Light Analyzer (GLA, version 2.0, Cary Institute of Ecosystem Studies, Millbrook, New York, USA) program (Frazer et al. 1999). Percent open sky does not specifically measure photosynthetic active radiation available to the forest floor vegetation especially in dissected landscapes, but will generally correlate with it (Comeau et al. 1998).

Vegetation sampling

Tree species were sampled by height and diameter and, for clarity in this paper, combined into four size classes and referred to henceforth as one of three regeneration classes or trees:

1. Small seedlings: stems <50 cm height.
2. Large seedlings: stems 50 cm height to 2.9 cm dbh.
3. Saplings: stems 3–9.9 cm dbh.
4. Trees: trees ≥ 10 cm diameter.

Vegetation was sampled in all four units in 2000 (Y0, before treatment), 2001 (Y1, first growing season after partial harvest and the first prescribed fire), 2004 (Y4, fourth growing season after the first treatments), 2006 (Y6, second growing season after the second fire), 2009 (Y9, fifth growing season after second fire), and 2013 (Y13, fourth growing season after third fire). At each gridpoint, small seedlings of all tree species were recorded within four 2-m^2 circular plots in the cardinal directions, centered 2 m from the center of the gridpoint. To increase the sample area for oak-hickory small seedlings, we sampled an additional 8.5-m^2 plot centered on the gridpoint for a total of 16.5 m^2 sampled per plot for oak-hickory.

Large seedlings and saplings (50 cm height to 9.9 cm dbh) were recorded in a 78.5-m^2 circular plot (5 m radius) centered on the gridpoint. By Y4, the HB units had dense thickets of woody stems in many areas, consisting of large seedlings of competitor species (e.g., yellow-poplar, *L. tulipifera*), stump sprouts (most notably red maple), and shrubs (e.g., *Rubus* spp., *Smilax rotundifolia*). Therefore, to make sampling more manageable in the HB units in Y4 and beyond, we reduced the area of sampling for a portion of large seedling size class (50–140 cm height) for the competitor species. We reduced the sampling area to the four 2-m^2 small seedling plots at each gridpoint, so that 8 m^2 rather than 78.5-m^2 areas were sampled. Throughout the study, we continued to sample large seedlings of oak-hickory within 78.5 m^2 of sampled area. For all large seedling, we recorded both the number of stems and the number of multiple-stemmed clumps of stump sprouts; for results reported here, we considered clumps as one individual rootstock and used number of individuals as the primary response variable in analyses.

Data analysis

Statistical treatments.—We used several procedures to summarize, analyze, and evaluate trends and treatment effects, as well as the relative status of the successional trajectories into the next forest. Regression approaches were used to uncover potential relations among the variables, using oak-hickory regeneration for the three size classes, but primarily large seedlings, as the response variable. We used linear regression, regression tree analysis (RTA), and RandomForest (Prasad et al. 2006) to determine major variables related to the abundance of small and large oak-hickory seedlings in Y13. Analyses were conducted in R (R Development Core Team 2008). Conditional XY plots were also used to elucidate trends in oak-hickory by year, IMI, and light level.

Using SILVAH:OAK to assess potential for oak-hickory regeneration.—We assessed the potential for successful oak-hickory regeneration on the HB units, using the "stocked plot" framework of SILVAH:OAK. The SILVAH:OAK decision support system was developed to help managers successfully regenerate oak stands in the mid-Atlantic region (Brose et al. 2008). Informed by previous studies of harvested stands, SILVAH:OAK uses a pre-harvest inventory of oak advance reproduction to recommend treatments for successful oak regeneration after a final removal harvest. Our data were not collected in a manner that could be directly imported into the SILVAH software. However, by scaling the regeneration data to average stem densities per unit area, we were able to make some general evaluations of the oak-hickory regeneration potential through time.

The SILVAH:OAK guidelines recommend that at least 50% of sample plots within a stand should be "stocked with competitive oaks" for oaks to maintain dominance after a final removal harvest; this translates to a density threshold of more than 1900 larger "competitive" oaks per ha on a majority of plots. In SILVAH:OAK, competitive oaks are >90 cm height; however, due to the size classes used in our study, we classify competitive oaks as >50 cm height (large seedling size class). We also include the hickories, in that they are similar to oaks, in having root-centered growth, intermediate shade tolerance, and hard-mast production.

Results

Overall stand density and canopy openness

In Y1, after partial harvesting and the first prescribed fire, overall stand density of trees >10 cm dbh was similar between the ZAL HB (mean = 253 stems/ha) and the REMA HB unit (mean = 262 stems/ha; Fig. 2). By Y13, following the 2nd and 3rd fires, stand density in ZAL HB was further reduced to a mean of 157 stems/ha, but it remained fairly similar among the dry, intermediate, and mesic IMI classes throughout the study (Fig. 2). By contrast, the variable intensity fires on the REMA HB unit resulted in sharply different stand densities across the landscape. By Y13, after the Y5 and Y10 fires burned at high intensity on the long southwest-facing slope of dry IMI class (Table 1), heavy overstory tree mortality reduced stand density to an average of just 70 stems/ha on dry sites and a final canopy openness of over 35% (Fig. 2). Stand density was also reduced sharply on intermediate sites, to 147 stems/ha. However, on the mesic sites located on the steep north-facing slope, stand density was only slightly lower in Y13 than in Y1 after the partial harvest. Over the 14 yr, the density for trees >10 cm was reduced for all species groups, including a 55% decrease in the oak-hickory and a 90% decrease in red maple (Appendix S1: Fig. S1). On the control units, stand density was stable over time, averaging 353 stems/ha across all years and similar to the densities prior to treatment on the HB areas (data not shown).

Reflecting the changes in stand density, canopy openness varied widely across treatments, years, and IMI class. On the control units, percent open sky was relatively constant across the 14 yr as expected, with dry sites slightly more open (5.4%) than mesic sites (4.3%), while intermediate sites averaged 4.9% (data not shown).

On the REMA HB unit, open sky averaged 6.0% in Y0 before treatments and continued to increase over time: Y1 (12.7%), Y6 (13.5%), Y9 (14.7%), and Y13 (22.4%). After the high-intensity fires on the southwest-facing slope in Y5 and Y10, variation among IMI classes was large; in Y13, dry sites averaged 35.9% open sky and mesic sites averaged 13.6% open sky (Fig. 2). Canopy openness reflects this topographic variation in fire intensity across the landscape (Fig. 3). Linear regression revealed an increasingly strong inverse relationship between % open sky and IMI through time on REMA HB: r^2 values were 0.002 ($P > 0.7$) in Y0 before treatment, 0.19 ($P < 0.001$) in Y1 after harvest and the first burn, 0.44 ($P < 0.001$) in Y6 and 0.45 ($P < 0.001$) in Y9 after second burn, and 0.51 ($P < 0.001$) in Y13 after third burn (Fig. 3).

On the ZAL HB unit, open sky averaged 7.0% in Y0 before HB treatment (Fig. 2). In contrast to REMA HB, the lower-intensity fires throughout ZAL HB resulted in less canopy openness (Fig. 2). Even though there was a near doubling of % open sky from Y0 to Y13, the majority of that increase occurred by Y1 after the initial partial harvest. ZAL started out in Y0 with a higher density of smaller trees, so that more trees needed to be cut to reach the desired level of basal area reduction. The repeated fires caused much less overstory mortality at this unit, as open sky exceeded 25% on only five of 60 plots. In a sharp contrast, more than half (46 of 71) of the plots exceeded 25% open sky on REMA HB unit by Y13. Linear regression showed that the inverse relationship between IMI and % open sky was significant but weaker at ZAL HB throughout the experiment, with the maximum r^2 value of 0.18 ($P < 0.001$) in 2009.

Tree regeneration response to partial harvest and burning

Oak and hickory.—Among all harvest and burn plots ($n = 132$), large oak-hickory seedlings (50 cm height to 2.9 cm dbh) increased dramatically, from a mean of 232 stems/ha in Y0 to 4081 in Y13 (Fig. 4), nearly a 18 × increase. Among IMI classes, the greatest increase in large oak-hickory seedlings was in the dry sites with an

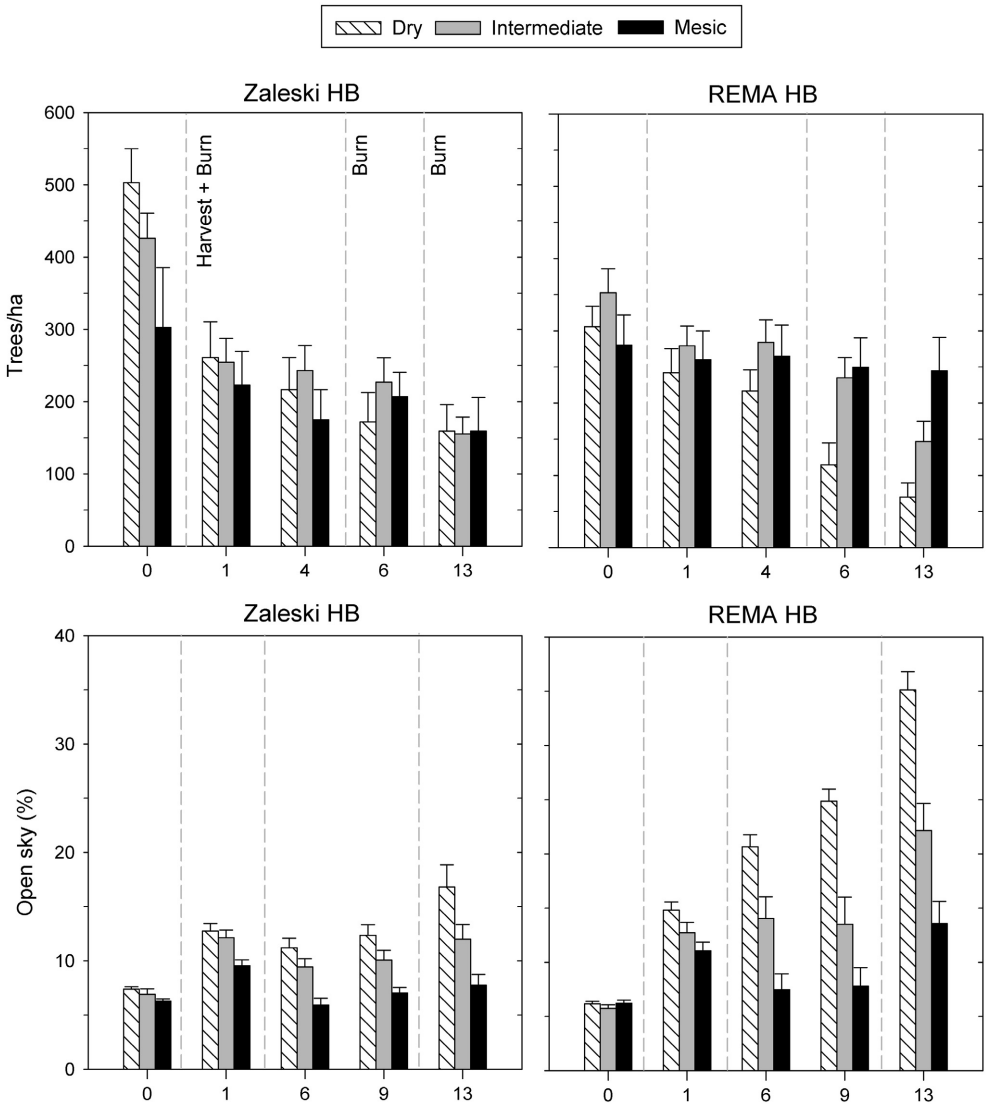

Fig. 2. Stand density for oak-hickory (trees >10 cm dbh per hectare) and percent open sky by year and IMI class (dry, intermediate, mesic) for the (A) REMA HB unit and (B) ZAL HB unit. *X* axis numbers refer to years following initial treatments. IMI, Integrated Moisture Index; REMA, Raccoon Ecological Management Area; ZAL, Zaleski; HB, harvest and burn unit.

initial 347 stems/ha in Y0 vs. 5801 stems/ha in Y13, and intermediate sites with 253 stems/ha in Y0 vs. 4657 stems/ha in Y13. Even on mesic plots, though, large oak-hickory stems increased from 58 stems/ha in Y0 to 1002 stems/ha in Y13. Thus, the proportional increases in density of large oak-hickory seedlings were similar among IMI classes, with a 17× increase on dry, a 19× increase on intermediate, and a 17× increase on mesic IMI classes (Fig. 4).

Maps of IMI, large oak-hickory regeneration, and canopy openness in Y0 vs. Y13 show the topographically controlled variation in stand structure and regeneration across the landscape, and highlight the importance of IMI in determining the level of large oak-hickory seedlings (Fig. 5). This topographic variation in open sky and oak-hickory regeneration is much more evident on the convex REMA TB unit, where there was almost a complete northeast-southwest

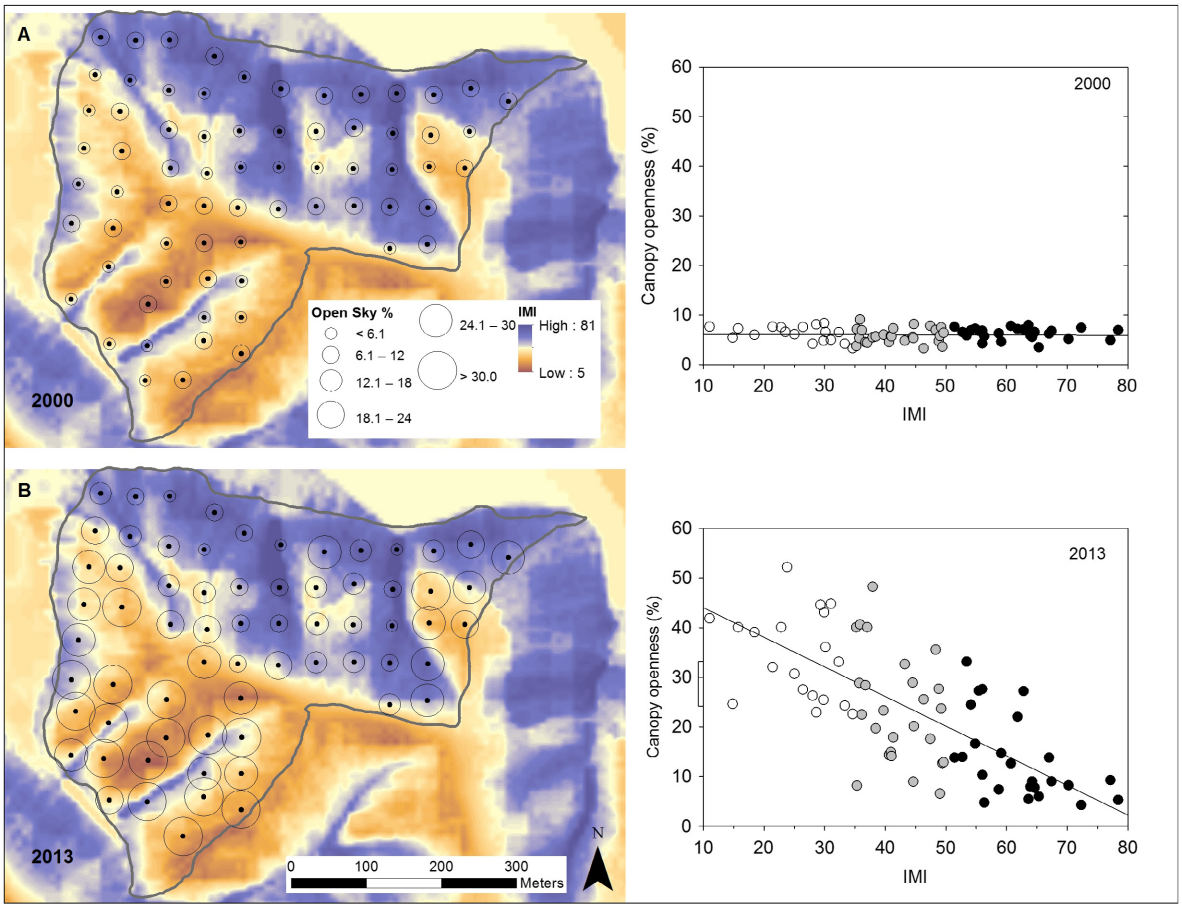

Fig. 3. Percent canopy openness by grid point for REMA HB unit, (A) before treatment (2000) and (B) after harvesting and three fires (2013). Openness averaged 6.0% in 2000 and 22.4% in 2013. Regressions show openness increasing over time for drier sites (lower IMI). Open circle = dry; gray circle = intermediate; solid circle = moist IMI class. IMI, Integrated Moisture Index; REMA, Raccoon Ecological Management Area; HB, harvest and burn unit.

dichotomy with highly varying IMI values (range 8–84, average 43.7, SD 15.2). REMA had maximum canopy openness and oak-hickory regeneration on the southwest, while very little regeneration occurred on the northeast, high IMI slopes (Fig. 1). In contrast was ZAL HB, which displayed a more homogeneous and slightly lower average (drier) distribution of IMI (range 14–76, average 39.5, SD 10.0). Consequently, fire treatments and resulting canopy openness were more homogeneous and with substantial oak-hickory seedlings throughout the stand except for the very bottom of the valleys (Figs. 1, 5).

Small (<50 cm height) oak-hickory seedlings also increased over time on the dry and intermediate IMI classes, particularly from Y4 (4 yr after the initial harvest and burn treatment) to Y9 (5 yr after the second fire). During that period mean stem densities increased from 12,400 to 24,210 stems/ha on dry plots and from 11,730 to 32,170 stems/ha on intermediate plots, respectively (Fig. 4). In contrast, mesic sites had much lower densities of small oak-hickory seedlings throughout the 14-year period. The density of oak-hickory saplings (stems 3–9.9 cm DBH) also remained very low (<50 stems/ha) across years, with essentially no stems on the mesic sites (Fig. 4).

Red maple.—Red maple showed a dramatic negative response to repeated fires; saplings (stems 3 to 9.9 cm DBH) decreased sharply after the initial treatment and were virtually eliminated by Y13. The great majority of saplings were topkilled by

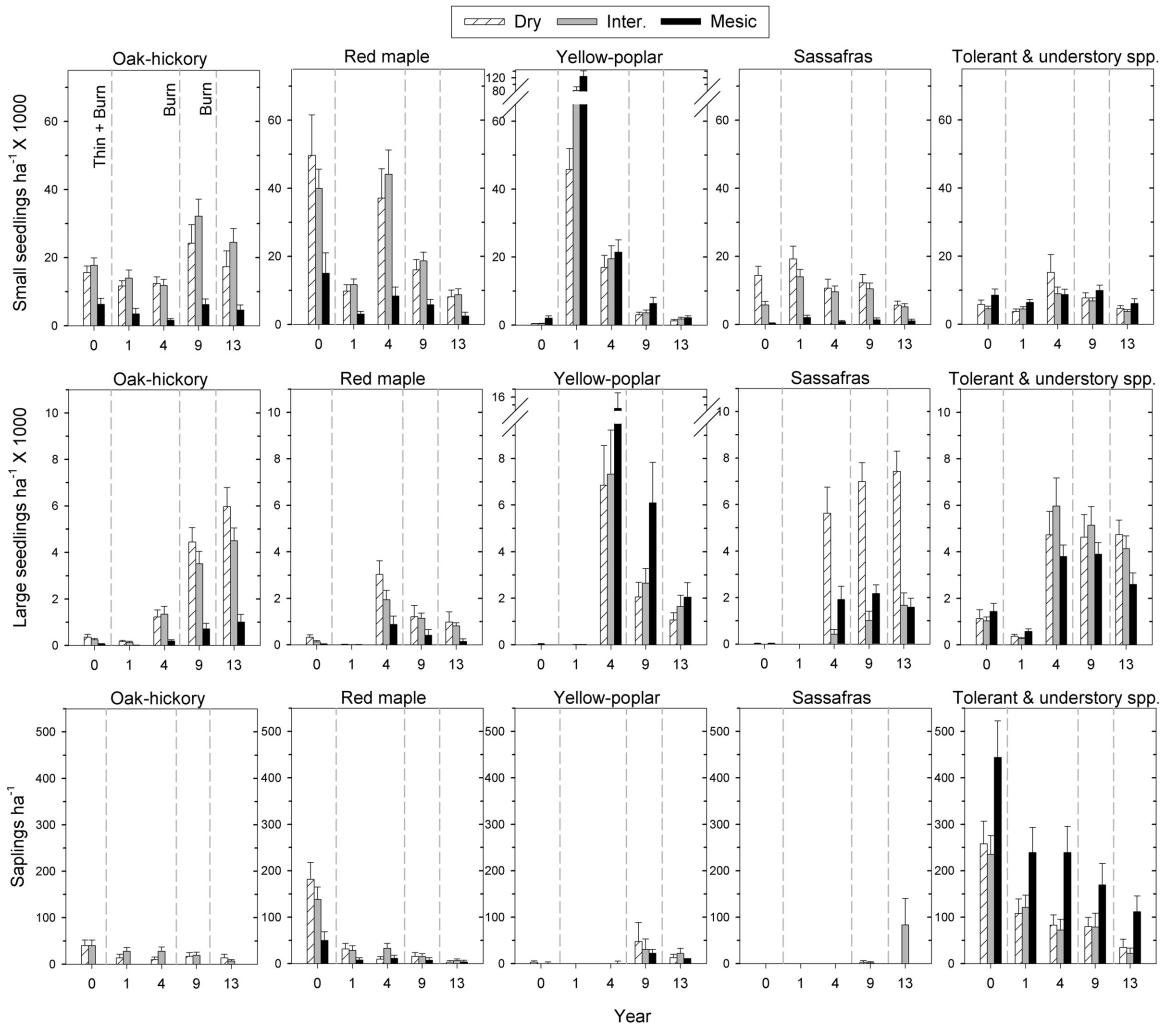

Fig. 4. Distribution of species groups by size class and Integrated Moisture Index moisture regime, 2000 (Y0) to 2013 (Y13). Fires occurred in spring Y1, Y5, Y10; sampling of regrowth occurred 1 yr (Y1), 4 yr (Y4), 2 yr (Y6), 5 yr (Y9), and 4 yr (Y13) after most recent fires.

fire because stems <15 cm dbh were generally not cut in the harvesting treatment. By Y4, large red maple seedlings (stems 50 cm tall to 2.9 cm dbh), many of which were sprouts of cut or burned saplings and pole-sized trees, had increased sharply, particularly on the dry and intermediate IMI class (Fig. 4). However, the 2nd and 3rd fires reduced the density of this size class by 65% between Y4 (mean = 1867 stems/ha) and Y13 (mean = 645 stems/ha). Small seedlings initially were stimulated by fire, but after each successive fire, the capacity for red maple seedling densities to rebound was reduced. By Y13, 4 yr after the 3rd fire, the density of red maple small seedlings was 81% less than in Y0.

Yellow-poplar.—Similar to red maple, yellow-poplar regeneration exhibited large increases, then decreases in density from Y0 to Y13 on the HB units (Fig. 4). Prior to treatments, the shade-intolerant yellow-poplar occurred at low densities in all regeneration size classes, but seed bank germination after the initial treatment resulted in very large numbers of small seedlings across all IMI classes. Peak densities reached an average of 123,000 stems/ha in mesic plots, more by far than any other species (Fig. 4).

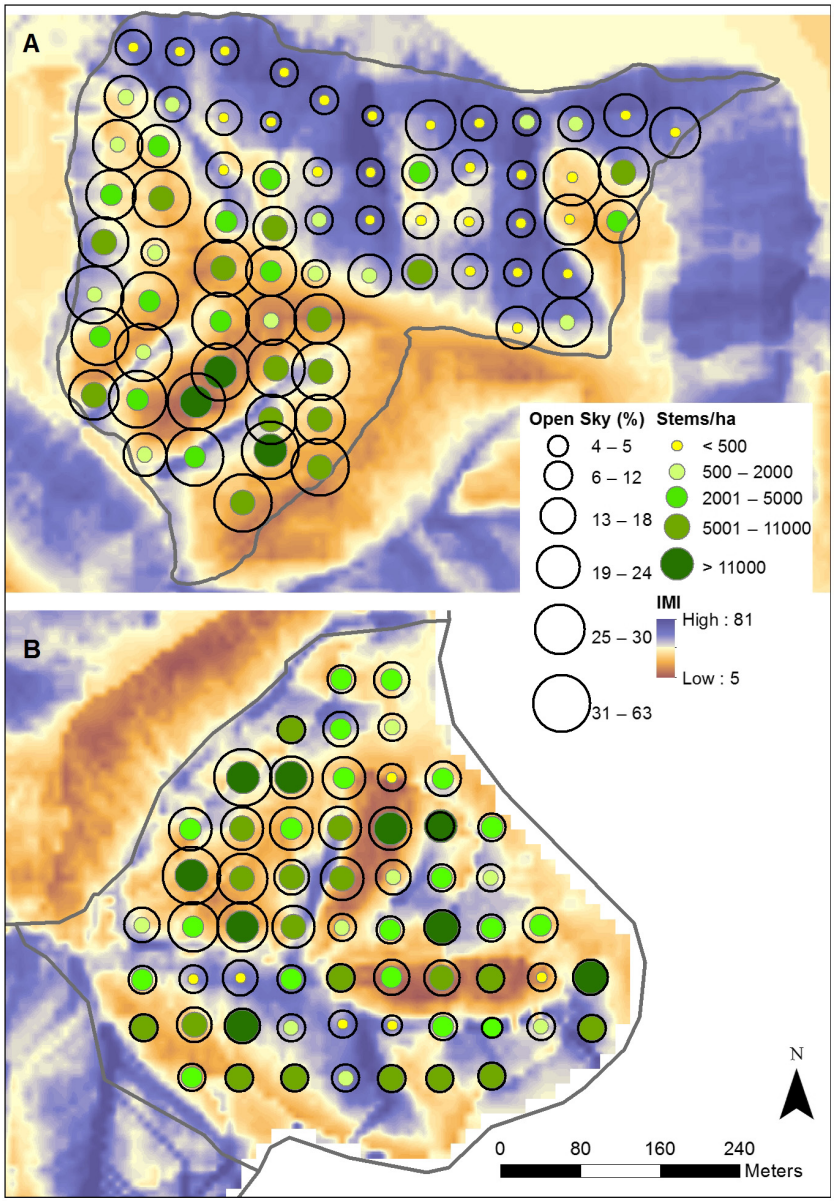

Fig. 5. Maps for (A) REMA HB and (B) ZAL HB treatment units. Percent open sky (size of rings), IMI, and oak-hickory stems/ha in 2013 (inside, colored circles). IMI, Integrated Moisture Index; REMA, Raccoon Ecological Management Area; ZAL, Zaleski; HB, harvest and burn unit.

However, the 2nd and 3rd fires resulted in sharp and cumulative decreases in seedling abundance. By Y4, the fourth growing season after initial treatments, many stems of the new yellow-poplar cohort had grown into the large seedling size class (50 cm tall to 2.9 cm dbh). However, by Y13, large yellow-poplar seedlings had been reduced 82% to 1464 stems/ha from the maximum in Y4 (8033 stems/ha). Yellow-poplar saplings (3–9.9 cm dbh) were present, but at very low densities (<50 stems/ha) by Y13, 4 yr after the 3rd fire.

Sassafras.—In sharp contrast to red maple and yellow-poplar, the density of large sassafras seedlings did not decrease after the second and third fires, still averaging >7000 stems/ha in Y13

(Fig. 4), indicative of fire tolerance. Prior to treatments, small sassafras seedlings (<50 cm) were abundant in the dry IMI class, averaging over 14,800 stems/ha but larger stems were rare (Fig. 4). Although the density of small sassafras seedlings remained relatively constant on the HB units throughout the experiment, there was a large recruitment of stems into the large seedling size class, mostly on the dry plots. By Y13, there was very little recruitment of sassafras to sapling status; it remains to be seen whether this occurs in coming years.

Shade-tolerant and understory species.—The group of shade-tolerant or understory species, taken collectively, responded to HB treatments with initial resprouting but subsequent reduction in sapling prominence following repeated fires. The major species in this group were as follows, in descending order of abundance: *Carpinus caroliniana* (musclewood), *Oxydendrum arboreum* (sourwood), *Hammamelis virginiana* (witch-hazel), *Nyssa sylvatica* (blackgum), and *Fraxinus americana* (white ash); together, these species comprised 76% of the stems in this group. Of these, only *F. americana* can typically attain canopy dominance; the others reside in the subcanopy or understory. Collectively, the tolerant and understory species were the most abundant species group in both the large seedlings and sapling size classes when the experiment began (Fig. 4). Small seedling densities remained relatively stable over time on the HB units. Similar to red maple, topkill after the initial burn treatment resulted in a large recruitment of sprouts into the large seedling size class by Y4. Unlike red maple, however, the later fires resulted in only modest additional density reductions by Y13. However, like red maple, the density of tolerant and understory saplings continued to decline following repeated fires (Fig. 4).

Trends in oak-hickory regeneration by canopy openness and soil moisture class

The increasing density of large seedlings (50 cm – 2.9 cm dbh) of oak-hickory was highly related to years post-initial treatment, post-fires light levels, and soil moisture (Fig. 6). We focus on this size class as critical for providing an adequate base for sustaining oak-hickory into the next forest. Fig. 6 clearly shows substantial increases in numbers of stems through time, but only if the canopy is opened up some and if the moisture regime is not highly mesic. Mesic plots rarely attained greater numbers regardless of light levels, but wherever open sky was >6% on intermediate and dry plots, there were substantial gains in large oak-hickory seedlings through time (Fig. 6). Most of the gains through time were in the 50- to 140-cm-height portion of large seedlings, where substantial gains were apparent by Y6 (Appendix S1: Fig. S1 and reported in Iverson et al. 2008). Gains in growth into the larger-sized fraction of large seedlings (140 cm – 2.9 cm dbh), those with a greater chance of advancing to the canopy, were not yet apparent in Y6 but started appearing in Y9, nearly a decade after initial treatment (Appendix S1: Fig. S2).

Regression tree analysis: factors related to the abundance of oak regeneration

Large seedlings of oak and hickory in 2013.—Regression tree analysis (RTA) emphasized that oak-hickory success depends on light, moisture, and competition, and it quantified some of these relationships. RTA revealed that low light resulted in very low densities of large oak-hickory seedlings (50 cm height – 2.9 cm dbh), but that higher light levels can encourage quite high densities by Y13. RTA of all 237 plots placed all control plots plus 18 HB plots in the same bin with the lowest oak-hickory density of 484 stems/ha (or ~1 plant every 20 m^2) when Y6–Y13 average open sky was <6%, regardless of other conditions (Appendix S1: Fig. S3). RTA on only the 130 HB plots showed that extremely low oak-hickory regeneration success was found (only 287 stems/ha) on 30 plots with low numbers of oak-hickory seedlings at the beginning of the experiment (small seedlings <8125 stems/ha) and when IMI was mesic (≥47; Fig. 7). However, the highest numbers (11,200 stems/ha, over 1 plant every m^2) were found if average open sky for Y6, Y9, and Y13 (SKYav6_13) exceeded 17%, if the number of initial seedlings exceeded 8125 stems/ha (again, usually on more xeric sites), and if competitive saplings in Y9 (compD2.409, 1.4 m height–2.9 cm dbh) were <4710 stems/ha (Fig. 7). Between these extremes, the success of oak-hickory depends on the levels of light, moisture, and competition (Fig. 7).

A separate RTA analysis was conducted which did not include prior abundance of oak-hickory,

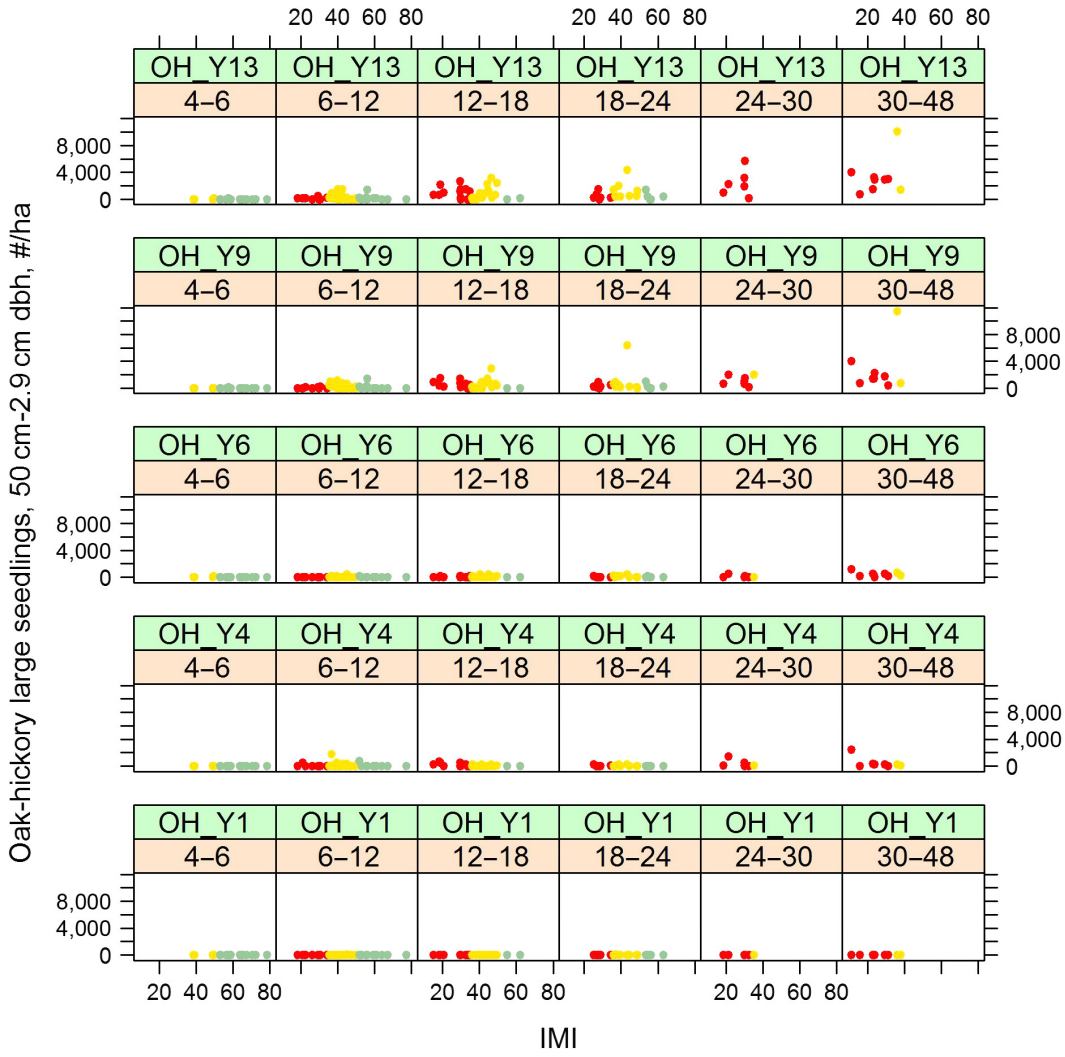

Fig. 6. Plots show changes in numbers, in trees per hectare, (*Y* axis) of large oak-hickory (OH) seedlings (50 cm – 2.9 cm dbh) through time after initial treatment (Y1–Y13 [2001–2013], *Y* dimension of trellis graph), by moisture regime (dry [red], intermediate [gold], mesic [green] IMI classes), also graded from 20 (dry) to 80 (moist) on *X* axis, and by % average open sky between Y6 and Y13 (4–48% open sky, *X* dimension of trellis graph). IMI, Integrated Moisture Index.

but did include competing plants (1.4 m height – 2.9 cm dbh). It revealed the "sweet spot" for oak-hickory regeneration numbers was when IMI was between 42 and 47 (mesic side of intermediate), the number of sapling competitors was held below ~7800 plants/ha, and the maximum open sky just after treatment was no more than 28% (Appendix S1: Fig. S4). On the other hand, few oak-hickory were present when plots were quite moist (IMI > 47 but especially when >56) and when competition was high. Of particular interest, the RTA provides some indication that opening up the canopy too much is not beneficial (especially if intense fires kill many overstory trees): There was a slightly higher number of oak-hickory when the maximum open sky during the Y6–Y13 period was below rather than above 28% (Appendix S1: Fig. S4).

Influence of sunlight and moisture on large seedlings of oak-hickory.—If all plant data were eliminated from the analysis so that only IMI values and open sky from Y0 to Y1 as well as

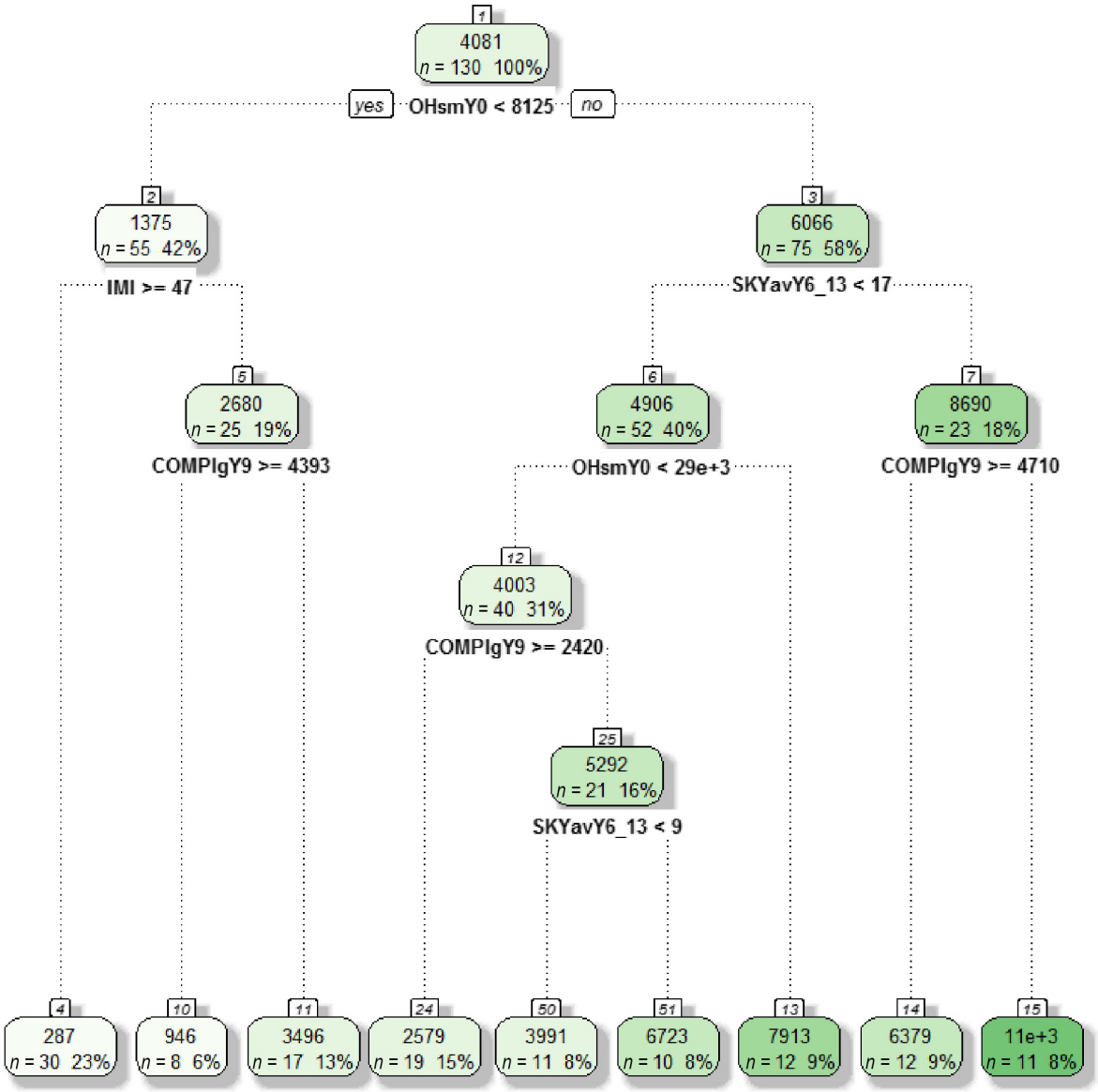

Fig. 7. Regression tree analysis diagram for the abundance of oak-hickory large seedlings per ha (50 cm height to 2.9 cm dbh) across only the HB plots (n = 130). Each box delineates stem density for large oak-hickory seedlings, number of plots in the analysis, and percent of plots falling into that bin. OHsmY0, oak-hickory small seedlings at year 0; IMI, Integrated Moisture Index; COMPIgY9, competing large seedlings at year 9; SKYavY6–13, average percent open sky measured at years 6, 9, and 13; HB, harvest and burn unit.

average open sky from Y6 to Y13 were considered, in this case for all 237 control and treatment plots, there emerged a clear trend that again emphasized the importance of adequate light and relatively drier conditions for good regeneration of oak-hickory. Maximum large seedlings of oak-hickory (50 cm height – 2.9 cm dbh) were found on plots with average open sky Y6–Y13 > 8.6%, IMI < 47 (intermediate and dry), open sky before treatment of >6.1%, and open sky after initial harvesting and fire treatments of >16% (Fig. 8). In contrast, with persistent closed canopy and/or mesic sites, low-regeneration success is expected. Similar trends were apparent

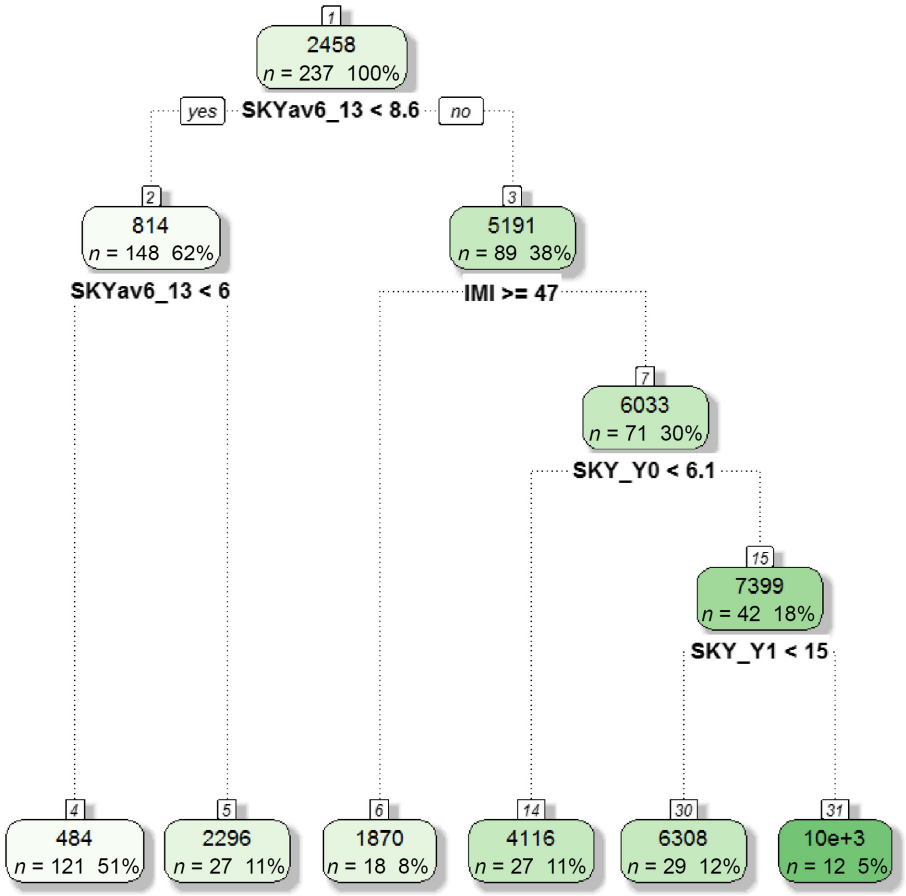

Fig. 8. Regression tree analysis diagram for the abundance of oak-hickory large seedlings (50 cm height to 2.9 cm dbh) across all plots (n = 237), and using only open sky and IMI variables. SKYavY6–13, average percent open sky measured at years 6, 9, and 13; IMI, Integrated Moisture Index; HB, harvest and burn unit.

when evaluating numbers of small seedlings (<50 cm height): Drier sites opened up to at least 10% open sky had the largest number of seedlings 13 yr later (figure not shown).

Using SILVAH:OAK to assess potential for oak-hickory regeneration

In Y0 prior to the treatments, only 2% of plots were stocked with competitive oak-hickory (hereafter, simply "stocked") by our comparison to the SILVAH:OAK regeneration guidelines (Fig. 9). Even on dry or intermediate sites, only three of 130 plots were stocked (all on REMA, Fig. 1). However, the percentage of plots that were stocked continued to increase over time with the harvest and repeated burning treatments. By Y13, 75% of the dry and intermediate plots were stocked across both REMA and ZAL (Figs. 1, 9), exceeding the 50% threshold in SILVAH:OAK for successful oak regeneration in a stand after removal of the canopy trees. In contrast on mesic sites, 21% of the plots became stocked by Y13, still a substantial increase (Figs. 1, 9). Spatially, the importance of topography is highlighted as the "center E-W spline" of REMA HB showed dramatic N–S variation, while the "bowl" of ZAL HB showed more even distribution of stocked plots (Fig. 1). The unstocked plots were almost exclusively found on northerly slopes or in valley bottoms with the highest IMI values.

Discussion

Sufficient stocking of large oak advance reproduction is required for future recruitment of

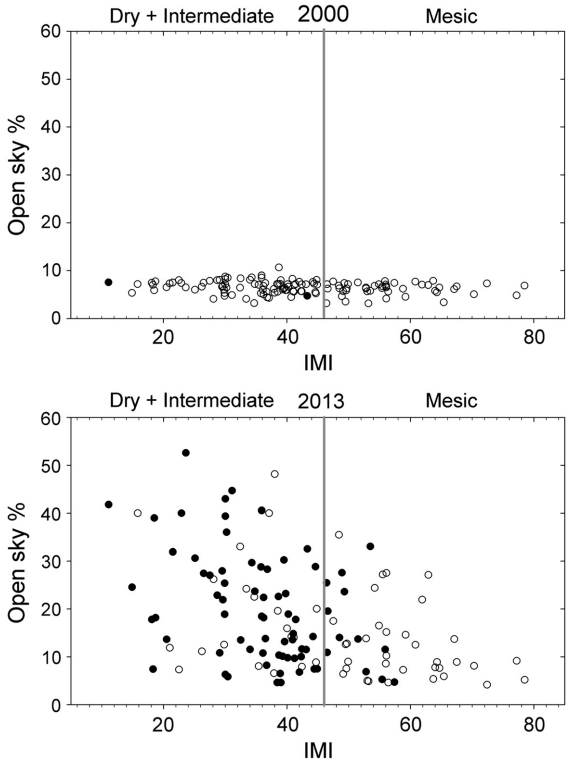

Fig. 9. Stocked (solid circle) vs. unstocked (open circle) plots with competitive oak according to SILVAH: OAK regeneration guidelines, with HB plots of IMI vs. % open sky prior to treatment (2000–Y1) and 13 yr after treatment (2013–Y13).

overstory oak (Sander 1972, Brose et al. 2008), but in most eastern oak forests, large oak seedlings are often sparse or absent. We found that a partial harvest and repeated fires, implemented over a 13-year period, increased the density of large (>50 cm height) oak-hickory seedlings, on average, by a factor of 18 across two sites in southern Ohio. Large stems of competing species also increased with the HB treatments, though repeated fires eventually reduced the abundance of two of the major competitors, red maple and yellow-poplar.

We also found that fire severity and tree regeneration dynamics were highly variable across the landscape. By sampling intensively on a 50-m grid, our findings emphasize the strong influence of topography on fire intensity and canopy openness, and also the response of oak-hickory regeneration across a range of moisture conditions and canopy openness.

Effects of partial harvest and repeated burning on tree regeneration

The partial harvest (~30% basal area reduction) and Y1 fires initially decreased the competitive position of oak-hickory regeneration as large stems of red maple, yellow-poplar, sassafras, and shade-tolerant/understory species became abundant by Y4, while oak-hickory did not (Albrecht and McCarthy 2006). The Y1 fires were conducted in the spring dormant season immediately after the winter harvest, and thus prior to the emergence of stump sprouts from cut trees, which were predominantly non-oaks. These stump sprouts, together with sprouts from shade-tolerant saplings topkilled by fire, then grew rapidly from Y1 to Y4 in the more open conditions created by the partial harvest. Harvesting and fire have been shown to provide favorable conditions for germination of seed-banking species such as yellow-poplar (Schuler et al. 2010). On our HB units, a large cohort of new yellow-poplar seedlings established in Y1, many of which grew into the large seedling size class by Y4. Recurrent fires are typically needed to kill the newly established seedlings of yellow-poplar and other species (Loftis and McGee 1993, Hutchinson et al. 2012, Brose et al. 2013, Waldrop et al. 2016). Indeed, the second (Y5) and third (Y10) fires in this experiment caused sharp reductions in the density of red maple and yellow-poplar in the large seedling size class, indicating significant mortality. During this same period (years 6–13), the abundance of large oak-hickory seedlings increased substantially in the higher light environment. Compared to most co-occurring species, oaks, which exhibit root-centered growth as seedlings, have been shown to have a stronger capacity to sprout repeatedly during a regime of multiple fires compared to non-oak competitors of similar size; and this sprouting ability of oak increases exponentially with increasing initial seedling size (Dey and Hartman 2005, Fan et al. 2012).

We also documented substantial increases in the abundance of small oak-hickory seedlings after the second fire in Y5, which were largely sustained through Y13 (Fig. 4). However, this effect was primarily manifested on the ZAL HB unit (not on the REMA HB unit) and the ZAL control unit also had a large and sustained increase in oak-hickory seedlings during this

period (data not shown); thus, this increase cannot be unequivocally attributed to fire but also to masting, especially from large mast crops of chestnut oak (Y5) and scarlet oak (Y7). There is, however, some evidence for fire improving the germination or survival of oak seedlings by providing an adequate seedbed for oak establishment through removal of litter (Carvell and Tryon 1961), reducing acorn pests (Riccardi et al. 2004), increasing nutrients (Kabrick et al. 2014*b*), xerifying the surface layer of soil (Barnes and Van Lear 1998), and/or increasing forest floor light. In similar forests in Kentucky, Royse et al. (2010) showed that while recent fires did not significantly increase the germination rates of oak seedlings after a mast event, survival of the new cohort of seedlings was greater on burned sites and was positively related to the greater light and lower litter depth found within the burned units.

Topographic moisture regime effects on oak-hickory regeneration, fire severity, and canopy openness

Not surprisingly, our data reiterate that the development of large oak-hickory seedlings was highly related to the topographic moisture regime. Although the greater abundance of oak regeneration on more xeric sites has been long established (e.g., Carvell and Tryon 1961, Loftis and McGee 1993), the IMI provides a gradient metric that can be linked to regeneration (Iverson et al. 1997, 2008). Mapping IMI and oak-hickory regeneration (Figs. 1, 5) further demonstrates the potential for predicting and planning for oak-hickory restoration. Interestingly, the "sweet spot" of large oak-hickory seedlings occurred when IMI was on the mesic side of the intermediate class (42–47), when the canopy was partially opened, and when competitor densities were not as prominent, confirming that oak-hickory grow better on more moist sites but high canopy cover and competition limit their abundance and accumulation on all but the drier sites. This conclusion was also reached by Kabrick et al. (2014*a*) in the Missouri Ozarks.

Though it is not yet known whether the resultant stocking on the dry and intermediate parts of the landscape (i.e., ridges, E–W–S slopes) will result in fully oak-stocked stands at maturity, the prevalence of large oak-hickory seedlings in concert with potential future silviculture treatments such as crop tree release at crown closure or intermediate stand thinning increases such a likelihood. However, these treatments will be much less effective in securing oak-hickory prevalence on the mesic parts of the landscape (i.e., N slopes, bottoms), to the point of recommending against such attempts. These conclusions are consistent with Nowacki and Abrams' (2008) observation that it is much more difficult to use fire to restore and maintain oak on fertile, mesic sites vs. infertile, xeric sites.

In the southern Appalachian Mountains, topography and weather conditions have been shown to have a strong impact on fire intensity and post-fire stand structure, with high-severity fires occurring in xeric landscape positions during extended dry weather conditions. Our study, in the less xeric mixed-oak forests of the Allegheny Plateau, showed that fire behavior and effects also varied substantially across the lower elevation but topographically dissected landscape. For example, the maps of open sky through time (Fig. 3) on the REMA HB unit revealed a close spatial relationship between moisture class and canopy openness, an indirect indicator of fire intensity, across the landscape. High-intensity fires on the long and steep SW-facing slope on the convex-shaped REMA HB unit resulted in substantial mortality of overstory trees which greatly opened the canopy, whereas the similarly steep but mesic north-facing slope on the REMA HB unit experienced lower-intensity fires that resulted in much less tree mortality and canopy opening.

The gridpoints on the steep SW-facing slope at REMA HB, that experienced high-severity fire, and the dry and intermediate gridpoints at ZAL HB (n = 52), that experienced low-severity fire, initially had similar mean densities of small oak-hickory seedlings in Y0 (REMA = 17,100 stems/ha, ZAL = 19,800 stems/ha). Thus, we can make a general comparison of the development of large oak-hickory seedlings under low- and high-severity fire regimes. On the concave-shaped and less steep ZAL HB unit, lower-intensity fires on the dry and intermediate gridpoints resulted in much lower canopy openness (13.5%) than on REMA HB (35.6%). Despite the large differences in fire intensity and the resultant stand structure, the mean density of large oak-hickory seedlings in

Y13 was quite similar, averaging 5680 stems/ha on the high-severity open-structured REMA HB gridpoints, and 6030 stems/ha on the low-severity, less open ZAL HB gridpoints. These results suggest that when adequate densities of small established oak-hickory seedlings are present initially, abundant large oak-hickory seedlings can develop across a wide range of fire severity and canopy openness. Canopy openness in the range of 6–18% (Fig. 6) was sufficient to promote oak-hickory regeneration. Opening the canopy above that, for example, >24% open sky through high-intensity fire, though also resulting in abundant large oak-hickory seedlings, is not necessary.

Overall, data provided here (e.g., Fig. 4; Appendix S1: Fig. S1) indicate that large oak-hickory regeneration can be developed with partial harvest and repeated burns on dry and intermediate sites. However, the effect of HB treatments on competing vegetation is also important.

Dynamics of competing vegetation

Landscape variability in soil moisture has a large impact on the vegetation competing with oak-hickories. In drier landscape positions, the competition was greatest from red maple, sassafras, yellow-poplar, blackgum, and sourwood. On mesic sites, the most abundant species were yellow-poplar, pawpaw (*Asimina triloba*), witch-hazel, and white ash; ferns and mesic forbs were also abundant. Similar edaphically driven variations in competitor species, particularly red maple on dry sites to sugar maple on moist sites, have been reported elsewhere in the absence of fire (e.g., Wisconsin: Nowacki et al. 1990, Pennsylvania: Nowacki and Abrams 1992).

The "super-generalist" red maple (Abrams 1998) is often the most intense competitor to oak-hickory regeneration in many areas of the Central Hardwoods, and sprouts vigorously following a harvest or a single fire (Albrecht and McCarthy 2006, Iverson et al. 2008, Schuler et al. 2013, Thomas-Van Gundy et al. 2015). However, we found that subsequent fires continually reduced abundance of red maple in the large seedling and sapling layers, and by Y13, most of the larger red maple stems had been eliminated; the thin bark of red maple makes it especially sensitive to heat damage and its sprouting capacity was reduced with multiple fires (Hare 1965, Harmon 1984, Hammond et al. 2015). Similar results on fire impacts on red maple were reported by Arthur et al. (2015) in Kentucky.

Sassafras seedlings became abundant by Y4 and sustained high densities through Y13. Clearly, the clonal sassafras, which often maintains an interconnected "seedling bank" on dry sites in mature oak forests, is stimulated by fire as sassafras regeneration exhibits low mortality and rapid growth after topkill by fire (Alexander et al. 2008). Although sassafras can attain overstory stature, the long-term competitive ability of sassafras on our study sites is unknown; it only rarely occurs today as an overstory tree in mixed-oak stands with a history of periodic fire during stand development, and it is generally viewed as a weak competitor (Hutchinson et al. 2008).

Although yellow-poplar was a minor species in the overstory on dry and intermediate sites, the initial harvest and burn stimulated abundant germination from the seed bank across the landscape. The density of yellow-poplar in Y1 averaged ~12 plants per m^2 on dry sites and about a third that density on mesic sites. These seedlings rapidly grew into the large seedling class, thereby creating an impenetrable thicket of plants. However after the later burns, seedlings were greatly reduced but still more abundant than before treatment, such that it is likely that a significant component of yellow-poplar will remain in the next forest (Fig. 4) unless severe drought conditions remove them (Hilt 1985). The dramatic decrease in yellow-poplar seedling densities with repeated fires in our study reflects the sensitivity of this species to fire (Brose and Van Lear 1998). On dry and intermediate plots, oak-hickory improved its competitive position relative to yellow-poplar throughout the course of the experiment; by Y13, large oak-hickory seedlings were several times more abundant than yellow-poplar (Fig. 4).

The tolerant/understory species group maintained relatively high stem densities in the large seedling size class after the later fires, particularly on dry and intermediate sites, where large oak-hickory also became abundant. Sourwood and blackgum comprised over half of the density on dry sites by Y13. While saplings of both species sprout vigorously, their long-term dominance will likely be limited due to slow radial growth and limited height growth (Burns and Honkala 1990, Abrams 2007). On intermediate sites, more species shared dominance, including

witch-hazel, musclewood, and white ash; none, however, are expected to greatly influence the capacity for oak-hickory to finally reach canopy in subsequent years.

Probability of successful oak-hickory regeneration

Based on the SILVAH:OAK "stocked plot" metric of oak competitiveness, we found that the HB treatments greatly increased the probability of successful oak-hickory regeneration by increasing the density of large advance reproduction. However, it should be emphasized that the large seedling size class (>50 cm height) was classified as "competitive," while SILVAH:OAK uses >90 cm height. Therefore, the estimates of competitive oak stocking that we report are almost certainly higher than if we had been able to apply the 90 cm threshold. An inspection of the maps of SILVAH:OAK "stocked" class vs. IMI (Fig. 1) and IMI vs. open sky (Fig. 3) shows visual spatial correlations, and although quite variable, those places with dry or intermediate IMI values (<47, Fig. 9) tended to have plots which were more competitive and stocked for oak-hickory regeneration. These plots also tended to have higher canopy openness, but as mentioned previously, we found that light levels >6% open sky were frequently sufficient for successful oak-hickory advancement. The maps also emphasize that a varied topography is important in creating heterogeneity in fire intensity when fire treatments are applied (e.g., Iverson et al. 2003), which consequentially adds to heterogeneity in species composition and structure, and thus more resilience to climate change or other disturbances (e.g., Lydersen and North 2012, Turner et al. 2013).

Conclusions and Recommendations

Despite decades of research, experimentation, and tools development (Johnson et al. 2009, Brose et al. 2014, Varner et al. 2016), successful oak-hickory regeneration at the landscape-scale remains difficult throughout much of the eastern United States. The multitude of natural and human values provided by oak-hickory communities underscores the need to further examine and refine the tools and techniques that encourage the sustainability of these forests, and to track the results over long periods. Especially under a changing climate, where models have shown oaks and hickories to be better suited to hotter temperatures and a more erratic moisture regime intensifying over the next decades (Clark et al. 2016, Iverson et al. 2016), the oak-hickory forest type must be promoted so that sources for propagules will remain throughout this century. We are encouraged by the results of this long-term study and have shown that partial harvests and repetitive burning can greatly bolster the chances of acquiring adequate stocking of competitive oak-hickory in the advanced regeneration. Because the treatment units had varied topography and were intensively sampled on a grid, we were able to document the response of oak-hickory regeneration across various levels of fire intensity, canopy openness, moisture regime, and pre-treatment seedling densities, thus providing unique evaluation of long-term effects of a wide suite of variables related to oak-hickory regeneration.

However, this study also highlights some of the challenges that managers face in facilitating oak-hickory regeneration across landscapes. Though treatments greatly increased the density of large oak-hickory seedlings, there also was ample competition from other species that also increased in the new treatment-based conditions. Also the high-severity fires that occurred on a portion of the landscape caused extensive mortality of large (mostly oak-hickory) overstory trees. Although these high-severity fire patches were not intended, they did allow us to document fire effects across a wide range of conditions. Even though large oak-hickory regeneration did occur in the high-severity burn area, large patches of overstory mortality are certainly not desirable if timber management is an objective. However, if timber management is not an objective, then patches of mixed-severity fires can serve to create a heterogeneous landscape, and that these "pyrodiverse" landscapes may eventually provide ecological benefits (Bowman and Legge 2016), especially in the face of an uncertain future of disturbances, including those directly or indirectly resulting from a changing climate (Dale et al. 2001, Vose and Elliott 2016) and the spread of forest pests (Ramsfield et al. 2016).

Eventually, it is important to undergo a fire-free period to allow the large oak-hickory seedlings to advance to larger size classes to gain fire resistance through diameter growth (Alexander et al. 2008, Knapp et al. 2015), and allow them a

reasonable probability of reaching the overstory as the current canopy dies or is removed. Arthur et al. (2012) estimated the necessary fire-free period, based on a minimum of 15 cm dbh, to be 10–30 yr depending on species, site quality, competition, and long-term retention of overstory trees.

Through partial harvest and burning treatments such as those demonstrated in this study, the development of large oak-hickory advance reproduction suggests an increased probability of having oak-hickory as a dominant component in the canopy of the next forest, but primarily on dry or intermediate sites. However, the dry and intermediate sites comprised 75% of the upland landscape.

Our key findings and recommendations include the following: (1) multiple fires are necessary to retard resprouting and regrowth of competing vegetation; (2) if timber management is the goal, care must be exercised to prevent excessively intense fires that kill many overstory trees, even the oak-hickory we wish to promote; (3) increase canopy openness to between 6% and 18%—less light prevents oak-hickory growth while greater light levels may favor shade-intolerant competitors; (4) oak-hickory regeneration success is much more likely on intermediate and dry moisture regimes (IMI < 47) and that implementing harvest and fire on mesic sites to promote oak-hickory regeneration is less likely to be practical; (5) patience is required in restoring oak-hickory—long-term management strategies and investments are required; and (6) for overstory recruitment, it is eventually necessary to remove fire for an extended period, depending on management objectives.

Acknowledgments

The authors are indebted to a host of field workers that helped make this possible, over the 14 yr of this study, especially the crew leaders, David Hosack, Kristy Tucker, Levi Miller, and Bill Borovicka, and the analysts for hemispherical photographs, Rebecca Wells and Tim Fox. Thanks also to Mike Bowden and the Ohio Division of Forestry for their lead in conducting the burns and harvest. We thank Tyler Refsland, Greg Nowacki, and the anonymous reviewers of Ecosphere for technical reviews which greatly improved the manuscript. Support is gratefully acknowledged from the National Fire and Fire Surrogate Research Project, the U.S. Joint Fire Science Program (JFSP), and the Northern Research Station.

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