COMPARISON OF OAK AND SUGAR MAPLE DISTRIBUTION AND REGENERATION IN CENTRAL ILLINOIS UPLAND OAK FORESTS

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Abstract.—Changes in disturbance frequencies, habitat fragmentation, and other biotic pressures are allowing sugar maple (*Acer saccharum*) to displace oak (*Quercus* spp.) in the upland forest understory. The displacement of oaks by sugar maples represents a major management concern throughout the region. We collected seedling microhabitat data from five upland oak forest sites in central Illinois, each differing in age class or silvicultural treatment to determine whether oaks and maples differed in their microhabitat responses to environmental changes. Maples were overall more prevalent in mesic slope and aspect positions. Oaks were associated with lower stand basal area. Both oaks and maples showed significant habitat partitioning, and environmental relationships were consistent across sites. Results suggest that management intensity for oak in upland forests could be based on landscape position. Maple expansion may be reduced by concentrating mechanical treatments in expected areas of maple colonization, while using prescribed fire throughout stands to promote oak regeneration.

INTRODUCTION

Historically, white oak (*Quercus alba*) dominated much of the midwestern and eastern U.S. hardwood forests (Abrams and Nowacki 1992, Franklin et al. 1993). Oak is classified as an early successional forest species, and many researchers agree that oak populations were maintained by Native American or lightning-initiated fires (Abrams 2003, Abrams and Nowacki 1992, Hutchinson et al. 2008, Moser et al. 2006, Nowacki and Abrams 2008, Ruffner and Groninger 2006, Shumway et al. 2001). These periodic low to moderate surface fires favored the ecophysiological attributes of oak over those of fire-sensitive, shade-tolerant tree species, thereby continually resetting succession and allowing oaks and other shade-intolerant species to persist in both the canopy and understory (Abrams 2003, Abrams and Nowacki 1992, Crow 1988, Franklin et al. 1993, Fralish 2004, Hutchinson et al. 2012). Initially, European settlers adopted the practice of burning hardwood forests (Nowacki and Abrams 2008). While these fires favored oak regeneration, logging by European settlers also removed the existing oak overstory, transforming an uneven-aged oak forest into an even-aged stand dominated by secondary growth white oak (Fralish et al. 1991, 1994; Franklin et al. 1993; Hutchinson et al. 2008).

By the early 20th century, nearly all of the remaining upland oak forest had endured some degree of compositional and structural transformation. Influenced by changes imposed by fire suppression policies and reductions in harvesting operations, understory environmental conditions shifted towards regeneration of shade-tolerant species (Ozier et al. 2006). The nearly continuous forested landscape became a series of smaller fragmented forest stands. After clearing for agriculture and urban expansion, eastern and Midwestern hardwood remnants were heavily dissected by roads, railways, cable cuts, and pedestrian pathways, further decreasing the frequency and magnitude of disturbance in these ecosystems (Nowacki and Abrams 2008).

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The present composition and health of upland oak-hickory forests are the result of biological and structural changes over the last four centuries (Oak 2006, Ruffner and Groninger 2006). Oak regeneration has nearly ceased due to 100 years of disturbance suppression, intensive deer browsing, and competition with native and exotic invasive plant species (Abrams 2003, Bowles et al. 2005, Hutchinson et al. 2008). Maple (*Acer* spp**.**), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), and other mesic species are placing strong competitive pressures on oak and hickory (*Carya* spp.) seedlings, and often have more success reaching sapling size (Fralish 2004). Even in oak-dominated stands where there are a substantial number of oak seedlings and no regeneration of late successional species, the current overstory and understory environments are still preventing oak survival into the next size class (Abrams and Nowacki 1992, Bowles et al. 2005, Haas and Heske 2005).

Historically restricted to mesic, nutrient-rich locations, late successional species are increasingly regenerating in the upland dry-mesic and xeric nutrient-poor sites traditionally dominated by white oak (Abrams 2003, Fan et al. 2012). Sugar maple (*A. saccharum*) and other fire-intolerant species have reached tree size in mesic stands and serve as a major seed source for recruitment into adjacent dry-mesic and xeric sites (Fralish 2004, Franklin et al. 2003). Understory shading caused by canopy closure, increased plant density in the subcanopy and understory, and the accumulation of a denser litter layer, may form moist, nutrient-rich microsites able to support sugar maple and similar species in formerly xeric or dry-mesic stands (Collins and Good 1987, Crow 1988, Franklin et al. 1993).

Forest managers fear that without silvicultural treatments, the white oak component of these forests will be replaced by sugar maple and other shade-tolerant species (Franklin et al. 1997, Moser et al. 2006). Some studies predict white oak may nearly disappear in many of the remaining upland forest tracts within the next 50 to 100 years (Fralish 2004, Franklin et al. 1993, Haas and Heske 2005). However, there is no clear consensus on the best management practices to use. Selecting one method or set of management practices to rescue the oak component in all upland forests may not be possible. It may be more practical to identify a set of environmental indicators that could be used to quantify the current health of the oak component in a stand. Linking an individual silvicultural practice or several with preidentified ranges of tolerance for these environmental indicators, could allow forest managers to more effectively choose an appropriate course of action to counter sugar maple expansion while restoring oak regeneration.

To identify how silvicultural treatments alter seedling-environment links, we surveyed five forests with different site histories and documented the microhabitat characteristics of individual seedlings. These data were used to determine (1) whether species of tree seedlings are selectively recruiting into specific microhabitats (habitat partitioning), (2) whether silvicultural treatment results in changes in microhabitat at the stand scale, and (3) whether silvicultural treatments alter seedling-environment relationships. The goal of this work was to determine the best stand locations for silvicultural treatment that will alter seedling-environment links towards those that favor oak regeneration and minimize maple regeneration.

METHODS

Field Sampling

From May to August 2007, study sites were established in forest stands at the U.S. Army Corps of Engineers' Lake Shelbyville Recreation Area in east central Illinois (39°32'17" N, 88°42'36" W). Data were collected from five upland oak forest sites differing in age class (old-growth vs. secondary growth) or management application (burned, thinned, or no treatment) (Table 1). Stands with trees 100 to 200 years old and free of signs of disturbance (e.g., tree stumps, canopy gaps, fire scars) were considered old-growth, and those with canopy trees 40 to 100 years old with evidence of disturbance were designated secondary-growth (Fralish et al. 1991). Forest overstory and understory measurements were taken at random points established along transects in each stand. Data were collected at least 30 m from a forest edge to minimize edge effects (Abrams and Nowacki 1992, Crow 1988, Parrott et al. 2012). A 10-factor prism gage was used at each random point to estimate the basal area (BA) per acre of standing trees in each stand and then converted to BA per ha (Table 1). Diameter at breast height (d.b.h.) was measured and species identified for each tallied tree. Understory data were collected in 50-m^2 circular plots and sapling data in 200-m^2 circular plots fixed with the random point at center.

Tree seedling species densities were measured by using the point-center quarter method at each random point (Abrams and Nowacki 1992, Collins and Good 1987, Hartman and McCarthy 2007). All individual seedlings <100 cm tall (15,592 stems) were identified to species, except for ash and hickory, which were identified only to genus. Red oak (*Q. rubra*) and black oak (*Q. velutina*) were difficult to distinguish when small, so these were grouped together. The presence, size, and position of maple and oak saplings taller than 100 cm and <6 cm d.b.h. were also recorded for each quadrant at the random points. Measurements were taken with standard forestry tools for percent canopy cover, litter depth (average of two ruler measurements), soil moisture, slope steepness, slope aspect, slope position, herbaceous cover, and shrub cover present at each random point and at the location of the nearest oak and maple seedlings (within 4 m in each quadrant). Point positions were recorded by using a hand-held global positioning system, and the presence of the exotic shrubs autumn olive (*Elaeagnus umbellata*) and honeysuckle (*Lonicera maackii*) was also noted.

Data Analysis

Standing tree data were used to calculate BA per ha for each species by random point and stand. Seedling BA and density per ha were determined for each stand and then used to calculate the relative density of each species in the understory. Slope position data recorded for each random point and

Table 1.—Description and history of the upland oak sites sampled at the Lake Shelbyville Recreation Area in Illinois, 2007

Stand	Area (ha)	Age class	Prescribed burn	Thinning	BA per ha
1	21.37	Secondary growth	No	Yes	23.9
2	16.80	Old-growth	Yes	No	24.4
3	20.26	Secondary growth	Yes	No	22.8
4	5.60	Secondary growth	Yes	No	27.9
5	17.99	Secondary growth	No	No	31.8

the associated closest oak and maple seedlings were separated into four categories based on landscape location: plateau, high, mid, and low. Slope aspects were grouped into three categories based on expected solar inputs: mesic, xeric, and plateau. We designated north, east, northeast, and northwest aspects as mesic, and south-,west-, southwest-, and southeast-facing positions as xeric at random points and at sampled oak and maple seedlings. Locations where no dominant aspect was observed were designated as plateau, the flat hilltop portion in each stand.

Statistical differences between tree distribution patterns and the effects of landscape position in the forest canopy and understory were analyzed by using a multivariate analysis of variance (MANOVA; SAS Version 9.1.3, SAS Institute Inc., Cary, NC) using the Wilk's Lambda test statistic. To test our hypothesis of habitat partitioning, the relative abundance of maples, white oak, and all oak species was related to slope aspect and position for both the understory and canopy layers. Relative densities of oak and sugar maple seedlings were compared among stands and the relative density of oak seedlings was correlated with BA per ha of overstory trees in each plot. A MANOVA was used to determine whether oak and sugar maple seedlings exhibited environmental selectivity. Environmental conditions recorded for each oak and maple seedling were compared to the measurements taken at each random point. A principal component analysis (PCA) ordination of the same environmental variables was used to visualize differences among sample points and stands in the MANOVA.

RESULTS

According to upland hardwood forest stocking guides by Roach and Gingrich, the five white oak-dominated stands sampled were fully stocked to nearly overstocked (U.S. Forest Service 2001). As would be expected, the stand that did not receive a thinning or prescribed burning treatment had the largest BA per ha (Table 1). Three of the four sampled stands receiving either a thinning or prescribed burn had noticeably smaller BA per ha (Table 1).

Slope position had a significant effect on tree distribution in both the understory and canopy layers in the sampled sites (Table 2). Although slope aspect did not have a significant effect on tree distribution in either the understory or canopy, the interactive effects of slope position and aspect did have a significant effect in the understory, showing finer environmental selectivity in the seedling stage (Table 2). Patterns of relative abundance in the canopy followed trends commonly associated with upland hardwood forests. Sugar maple was more abundant on lower slope positions and mesic

Table 2.—Effects of landscape position on tree distribution in the understory and canopy forest layers on sites at Lake Shelbyville Recreation Area, Illinois, with significant P-values in bold (results from a MANOVA test using Wilks' Lambda statistic)

Effect	F-Value	P > F
Understory		
Slope position	4.26	**<0.0001**
Slope aspect	1.65	0.1318
Slope position × aspect	2.05	**0.0189**
Canopy		
Slope position	2.46	**0.0097**
Slope aspect	1.29	0.2549
Slope position × aspect	0.48	0.9289

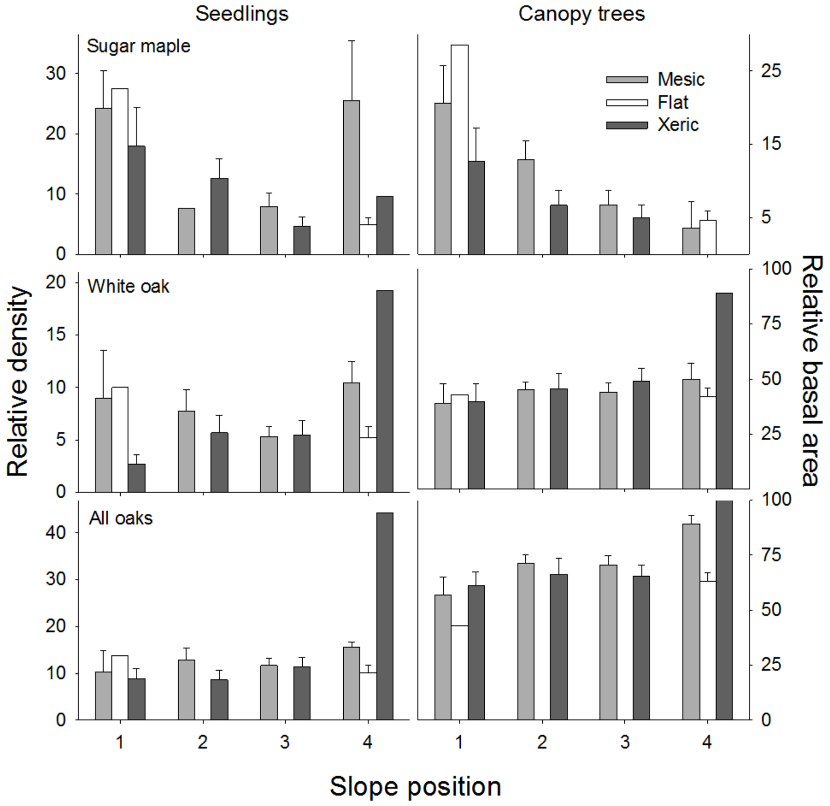

Figure 1.—Effect of slope position and aspect on the distribution of oak and maple in the forest understory and canopy. Slope position – 1: low, 2: mid, 3: high, 4: plateau.

aspects (Fig. 1). In contrast, the distribution of white oak and all oak species combined was fairly constant regardless of slope position or aspect, with only a slight increase in abundance on higher slope positions.

Patterns of overstory tree distribution differed from those in the midstory and understory. Occurrences of sugar maple saplings were higher than all oak species in each stand, suggesting that maple seedling survival rates into the next age class were much higher in our study areas. The number of sugar maple saplings exceeded that of combined oak species by ≥81 percent in stands 1, 3, and 5 whereas sugar maple outnumbered oaks in stand 2 by only 35 percent and in stand 4 by only 12 percent.

We observed 332 sugar maple seedlings and 276 white oak seedlings across the five studied stands, with sugar maple and white oak relative densities reaching 8.65 and 5.97 individuals per 50 m^2, respectively. The observation of sugar maple and white oak in the understory was nearly equal in stands 1, 2, and 4. However, we recorded the presence of about twice as many sugar maples as white oaks in stands 3 and 5. We expected to find more sugar maple in the understory of stand 5 because it did not receive either a thinning or prescribed burning treatment. However, in stand 3 we observed only six sugar maples in the overstory, which were 76 to 89 percent fewer observations than in the other four stands. Sugar maple seedling densities were highest in the lower slope positions regardless of slope aspect, but also showed a remarkable increase on mesic aspects in the plateau portions of the sampled stands (Fig. 1). White oak and all oak seedlings combined were fairly uniform across all slope positions and aspects in the understory, similar to the overstory pattern. In contrast with sugar maple, the highest densities of oak seedlings were observed on the xeric aspects of the plateau in each stand (Fig. 1).

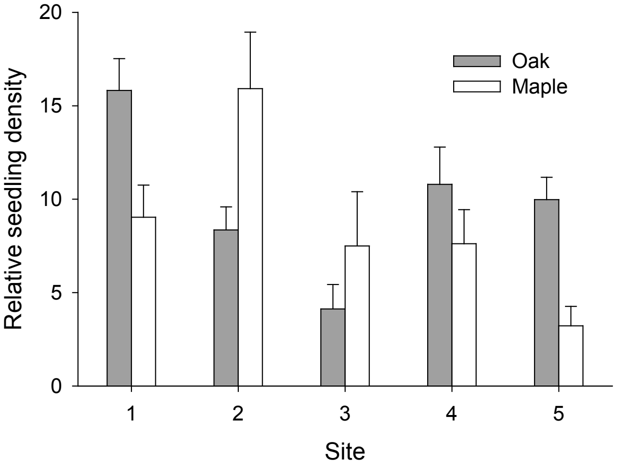

Figure 2.—Oak and maple seedling densities across study sites. 1: thinning, 2-4: prescribed burn, 5: no treatment.

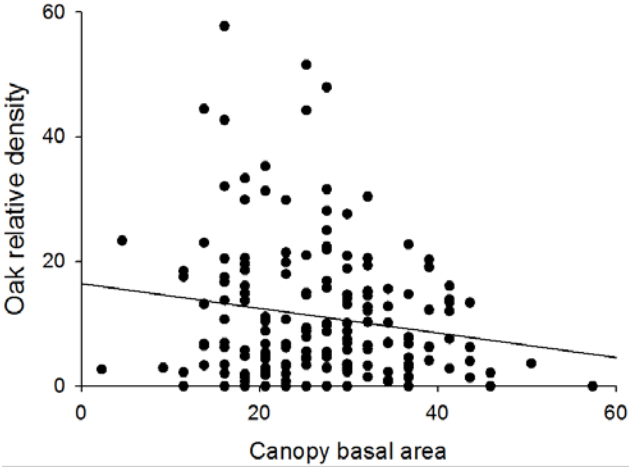

Figure 3.—Relative density of oak seedlings as a function of basal area of overstory trees.

There were marked differences in oak and maple seedling densities across forest stands. Oak relative densities were the highest in stand 1, where a thinning treatment occurred about 13 years before our study (Fig. 2). Oak seedling densities also remained higher than sugar maple in stands 4 and 5. Even though stands 2 and 3 received a prescribed burn, sugar maple seedling densities were nearly double those of oak seedlings in stand 3 (Fig. 2). Ten of the 12 sampling locations in stand 3 were located on either high or plateau slope locations, suggesting that this area was susceptible to adjacent sources of wind-blown maple seeds. We expected oak seedling densities to increase as the BA per ha of overstory trees decreased (Fig. 3). There was overall a significant negative correlation (R = -0.16; P = 0.028) between canopy BA and oak seedling relative density. When we analyzed the effect separately for each stand, however, there was a significant correlation only in stand 4.

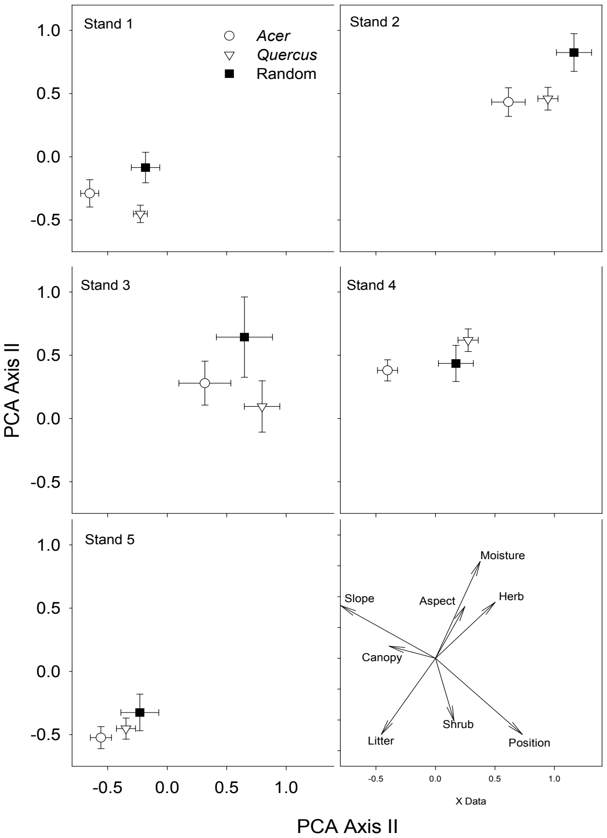

Figure 4.—Environmental selectivity of oak and maple seedlings in relation to random points. Data come from a PCA ordination of environmental variables. Lower right panel portrays the loading of each environmental variable on the PCA.

The results of the PCA showed that microclimatic conditions differed appreciably among stands. The PCA of seedling and random microhabitats resulted in two informative axes (eigenvalues >1) and explained 25.0 and 17.7 percent of the variation in the data set, respectively. However, oak and maple seedlings were consistently separated from each other and from random data points in each stand (Fig. 4, Table 3). Contrasts in the MANOVA revealed significance in random versus *Acer* points (P < 0.0001) and *Acer* versus *Quercus* points (P < 0.0001) along the first PCA axis. Sugar maple and oak did not differ from each other on the second PCA axis (P = 0.9792), but both differed from random points (P = 0.0099 and P = 0.0075, respectively). The stand × species interaction was not significant, suggesting the direction

Table 3.—Habitat specificity in maple and oak seedlings sampled on sites at Lake Shelbyville Recreation Area, Illinois, relative to random points, with significant P-values in bold (results from a MANOVA test using Wilks' Lambda statistic)[a]

Effect	F-Value	P > F
Stand	61.95	**<0.0001**
Species	14.42	**<0.0001**
Stand × species	1.46	0.1058

[a] Visualization of these data is presented in Figure 4.

of habitat selection was consistent. Environmental shifts from random points were similar in stands 1 and 5, but with slightly greater effects from canopy and shrub coverage in stand 1. In stands 2 and 3, maple appeared influenced most by aspect and moisture, whereas oak displayed additional effects from slope position. Oak and maple separated along environmental gradients most notably in stand 4. As in stands 2 and 3, aspect and moisture appeared the most influential on oak site selection. In contrast, maple appeared most affected by slope and canopy cover conditions.

DISCUSSION

Although BA per ha was noticeably smaller in three of the stands receiving silvicultural treatments, the fact that they remained at fully stocked levels suggests they did not have the canopy openness needed to promote competitive oak regeneration (Hutchinson et al. 2008, Moser et al. 2006). The higher BA per ha in stand 4 could be explained by the stand's size (5.6 ha), shape (rectangular), and surroundings (row crop agriculture fields). This stand configuration could promote colonization from wind-dispersed seeds and intensify seed predation rates on acorns (Haas and Heske 2005, Hutchinson et al. 2008), even though the narrowness of the tract would have increased light penetration into the forest interior (Shotola et al. 1992).

The responses of maples and oaks to slope position and aspect were comparable to other studies (Abrams 2003, Fralish 1994, Fralish et al. 1991, Ozier et al. 2006) and may explain differences among stands in relative abundance. The higher numbers of sugar maple in stand 3 could be related to the abundance of favorable mesic conditions facilitated by dense canopy layers in the overstory and midstory. Growth and survival patterns of saplings in the midstory have been documented to cause shifts in species composition of tree seedlings during succession (Delucia et al. 1998, Fan et al. 2012). Dominance of maple in the subcanopy restricts solar inputs to the understory, causing an increase in competition intensity that favors shade-tolerant species (Bowles et al. 2005, Franklin et al. 1993). This effect appears prominent as sugar maple slowly colonizes upslope and across moisture gradients into areas traditionally less suitable for this species. Light restrictions imposed by adjacent maple canopy and subcanopy trees, along with a denser maple leaf litter resistant to disturbance (e.g., fire, insect herbivory), facilitate an increase in mesic germination sites that favors further maple seedling establishment (Franklin et al. 2003). Maple expansion patterns across both moisture and slope gradients increase direct competition with oak, reducing the ability of oak seedlings to reach sapling size (Adams and Anderson 1980, Ozier et al. 2006).

Successful oak regeneration has been linked to forest disturbance and lower stocking rates (Abrams 2003, Bowles et al. 2005, Crow 1988), so we assumed oak seedling densities would be highest in stands with disturbance and smaller BA per ha of canopy trees. Although this pattern remained true in two of the four stands receiving a silvicultural treatment, the lack of oak recruitment into the sapling class across all sites suggests that a future species shift in overstory dominance will occur. Numerous studies suggest stand thinning by individual tree selection, as opposed to group selection, provides maple with a lifelong advantage over seedlings and saplings of oak, which needs direct sunlight throughout its life (Fralish 2004, Nowacki and Abrams 2008, Ozier et al. 2006). In addition, the positive effects of fire without canopy disturbance on oak regeneration may be short lived and not sufficient to disrupt the successional trends toward shade-tolerant species (Abrams 2003, Franklin et al. 2003, Nuttle et al. 2013).

Microsite habitat segregation between oaks and maples at the stand level was consistent with other studies that have documented similar shifts along environmental gradients between tree species (Collins and Good 1987). Although oak is tolerant of a wide range of environmental conditions, limited mostly by light levels and disturbance, maple requires mesic habitats driven by an intact canopy and subcanopy with a denser developed understory (Horsley et al. 2002, Nigh et al. 1985). Most importantly, the environmental shifts generated by maple dominance in the canopy will specifically shift the understory environment towards microenvironments that favor maple seedlings. In these forest stands, oak may be simply surviving in the microsites available as sugar maple alters environmental conditions; these changes reduce disturbance and facilitate moister, cooler microsites—further reducing the ability of oak to recruit into the next size class (Nowacki and Abrams 2008). In addition, the consistency of environmental preferences among stands suggests that silvicultural treatments have not altered the underlying physiological constraints on tree regeneration.

Seedling responses in this system suggest that there are different physiological mechanisms involved in regulating oak and maple regeneration. Maple species appear to be selectively recruiting into specific microhabitats that are subsequently altered towards environmental conditions that further promote maple regeneration. In contrast, oak regeneration seems to be more responsive to changes in microhabitat imposed by silvicultural disturbances. Silvicultural treatments can alter understory environmental conditions, and can provide increased opportunities for oak regeneration. However, results of this study indicate that single thinning or fire prescriptions are insufficient to restrict maple to preferred environments. Several studies suggest using prescribed burns before and after group selection thinning, which would promote oak seedling root development while culling current sugar maple regeneration (Crow 1988, Delucia et al. 1998, Franklin et al. 1993, Haas and Heske 2005, Hutchinson et al. 2008, Moser et al. 2006, Ruffner and Groninger 2006). The effects of slope and aspect on patterns of maple and oak regeneration in our study support the argument that land managers could use landscape position to pinpoint silvicultural treatments at the stand level. Because maples and other shade-tolerant species have shown the ability to stump sprout (Hutchinson et al. 2008, Tift and Fajvan 1999) and achieve sapling sizes resistant to fire, maples in the subcanopy should be both mechanically and chemically culled (Hutchinson et al. 2012). Maple expansion may be reduced by concentrating mechanical treatments in expected areas of maple colonization, while continually using fire throughout stands to promote oak regeneration. By effectively targeting management efforts, land managers may focus on those sites most likely to result in increased oak regeneration.

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