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Comparison of Oak and Sugar Maple Distribution and Regeneration in Central Illinois Upland Oak Forests

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

BY

PETER J. FREY

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE – BIOLOGICAL SCIENCES

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2014

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ABSTRACT

Although white oak (*Quercus alba*) dominated much of the mid-west and eastern US hardwood forests prior to European settlement, changes in disturbance frequencies and habitat fragmentation, coupled with other biotic pressures, are allowing sugar maple (*Acer saccharum* Marshall) to displace oak in the upland forest understory. Since our understanding of how disturbance mechanisms influence oak regeneration is not fully clear, there is lack of consensus on how to employ management practices. We collected seedling microhabitat data from 5 upland oak forest sites in central Illinois, each differing in age class and/or silvicultural treatment to determine: 1) Whether species of tree seedlings are selectively recruiting into specific microhabitats, 2) Whether silvicultural treatment results in changes in microhabitat at the stand scale, and 3) Whether silvicultural treatments alter seedling-environment relationships. Despite different management histories, oak and maple seedling densities were not significantly different among sites. Results of a MANOVA showed significant relationship between understory oak and maple distributions with slope position (<0.0001) and a slope × aspect interaction (0.0189). Maples were more prevalent in mesic slope and aspect positions. A PCA for environmental variables followed with MANOVA by site showed the environmental relationships among species was consistent across sites. At each site, oaks typically separated from sugar maples suggesting environmental variables influence distribution regardless of site history. 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 continually using fire throughout stands to promote oak regeneration.

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INTRODUCTION

Historically, white oak (*Quercus alba* L.) dominated much of the Midwest and Eastern US hardwood forests (Abrams and Nowacki 1992; Franklin et al. 1993). Classified as an early successional forest species, many agree oak populations were maintained by Native American or lightning initiated fires (Abrams and Nowacki 1992; Shumway, Abrams, and Ruffner 2001; Abrams 2003; Moser et al. 2006; Ruffner and Groninger 2006; Hutchinson, Long, and Sutherland 2008; Nowacki and Abrams 2008). These periodic low to moderate surface fires favored the ecophysiological attributes of oak over 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 (Crow 1988; Abrams and Nowacki 1992; Franklin et al. 1993; Abrams 2003; 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 to a secondary growth, even-aged white oak dominated stand (Fralish et al. 1991; Franklin et al. 1993; Fralish 1994; 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 shade tolerant species' regeneration (Ozier, Groninger, and Ruffner 2006). The nearly continuous forested landscape became a series of smaller fragmented forest stands. Cleared for agriculture and urban expansion, eastern and mid-western 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).

The present composition and health of upland oak-hickory forests are the result of the biological and structural changes endured during the last four centuries (Oak 2005; 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, ash, elm, and other mesic species are placing strong competitive pressures on oak and hickory seedlings, often having more success reaching sapling size (Fralish 2004). Even in oak dominated stands where there are a substantial number of oak seedlings and no late-successional species regeneration, 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 (*Acer saccharum* Marshall) 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 (Franklin, Robertson, and Fralish 2003; Fralish 2004). 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, micro-sites 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 treatment, the white oak component of these forests will be replaced by sugar maple and other shade tolerant species (Franklin, Robertson, and Fralish 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 (Franklin et al. 1993; Fralish 2004; Haas and Heske 2005). However, there is no clear consensus on the best management practices to employ. Selecting one method or a set of management practices to rescue the oak component in all upland forests may not be plausible. 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 individual or several silvicultural practices with pre-identified 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 linkages, five forests with different site histories were surveyed and the microhabitat characteristics of individual seedlings were documented. 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 linkages 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, USA (39°32'17"N, 88°42'36"W). Data were collected from 5 upland oak forest sites, each differing in either age class (old-growth vs. secondary-growth) or management application – burned, thinned, or no treatment (Table 1). Increment cores were taken to determine average tree age. Stands with trees 100 to 200 years old and free of signs of disturbance (tree stumps, canopy gaps, fire scars, etc.) were considered old-growth, while those with canopy trees aging from 40 to 100 years old with evidence of disturbance were designated secondary growth (Fralish et al. 1991). Soils were similar at each site, consisting of Miami Loam, Senachwine Silt Loam, and Xenia silt loam (United States Department of Agriculture 2014). Random points were established along transects in each stand; the total number of points and transects was determined by acquiring at least a 10% basal area (BA) sample of the total site. Forest overstory and understory measurements were taken at each random point. Data collection was conducted at least 30 m from a forest edge to minimize edge effects (Crow 1988; Abrams and Nowacki 1992; Parrott et al. 2012). A 10 basal area per foot (BAF) prism gage was used at each random point to estimate the BA per acre of standing trees in each stand and then converted to BA per ha (Table 1). The diameter at breast height (dbh) was measured and species identified for each tallied tree. Understory data was 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 using the point-center quarter method at each random point (Collins and Good 1987; Abrams and Nowacki 1992; Hartman and McCarthy 2007). All individual seedlings less than 100 cm tall (15,592 stems) were identified to species, except for ash (*Fraxinus* spp.) and hickory (*Carya* spp.), which were only identified to genus. Since red oak (*Quercus rubra* L.) and black oak (*Quercus velutina* Lam.) 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 less than 6 cm dbh were also recorded for each quadrant at the random points. Using standard forestry tools, measurements were taken 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 using a hand held GPS and the presence of the exotic shrubs autumn olive (*Elaeagnus umbellata* Thunb.) and honey suckle (*Lonicera maackii* Rupr.) were also noted.

Data Analysis

Standing tree data was used to calculate BA per ha for each species per random point and stand. Seedling BA and density per acre 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 the associated closest oak and maple seedling 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. North, east, northeast, and northwest aspects were designated mesic, while south, west, southwest, and southeast facing positions were considered xeric at random points and sampled oak and maple seedlings. Locations where no dominant aspect was observed were designated as plateau, the flat hill top portion in each stand.

Statistical differences between tree distribution patterns and the effects of landscape position in the forest canopy and understory were analyzed using a multivariate analysis of variance (MANOVA; SAS version 9.1.3) using the Wilk's Lambda test statistic. To test the 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 Components 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 (U.S.Forest Service 2001), the five white oak-dominated stands sampled were fully stocked to nearly overstocked. 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).

In all the sampled sites, slope position had a significant effect on tree distribution in both the understory and canopy layers (Table 2). While slope aspect did not have significant effects 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 aspects (Figure 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. Sugar maple saplings were observed 81% or more than the combined oak species in stands one, three, and five; whereas sugar maple only outnumbered oaks in stand two and four by 35% and 12% respectively. Calculated relative sapling densities differed slightly from oak and maple sapling counts, most notably in stand 4 (Figure 2). Although maple sapling populations exceeded those of oak in the entirety of stand 4, maple saplings only outnumbered oak at 16 of the 43 sampled points. This pattern could suggest that oak and maple species are separating along environmental gradients available at the stand level.

We observed a total of 332 sugar maple seedlings to 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 one, two, and four. However, we recorded the presence of approximately twice as many sugar maples than white oaks in stands three and five. We expected to find more sugar maple in the understory of stand five since it did not receive either a thinning or prescribed burning treatment. However, in stand three 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 (Figure 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. The highest densities of oak seedlings were observed on the xeric aspects of the plateau in each stand, opposite to the pattern of sugar maple (Figure 1).

There were marked differences in oak and maple seedling densities across forest stands. Oak relative seedling densities were the highest in stand one where a thinning treatment occurred approximately 13 years prior to our study (Figure 3). Oak seedling densities also remained higher than sugar maple in stands four and five. Even though stands two and three received a prescribed burn, sugar maple seedling densities nearly doubled oak seedlings in stand three (Figure 3). Ten of the 12 sampling locations in stand three were located on either high or plateau slope locations, suggesting this area was susceptible to adjacent seed sources of wind-blown maple seeds. As expected, oak seedling densities increased as the BA per ha of overstory trees decreased (Figure 4). There was an overall significant negative correlation ($R=-0.16$, $P=0.028$, Pearson correlation with 178 degrees of freedom) between canopy BA and oak seedling relative density. However, when the effect was analyzed separately for each stand, there was only a significant correlation in stand four.

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 over 1) and explained 25.0% and 17.7 % 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 (Figure 5; Table 3). Contrasts in the MANOVA revealed significance in random points verses *Acer* points ($P<0.0001$) and *Acer* points verses *Quercus* points ($P<0.0001$) along the first PCA Axis. Sugar maple and oak did not differ from each 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 of habitat selection was consistent. Environmental shifts from random points were similar in stands one and five, but with slightly greater effects from canopy and shrub coverage in stand one. In stands two and three, maple appeared influenced most by aspect and moisture, while oak displayed additional effects from slope position. Oak and maple separated along environmental gradients most notably in stand four. As in stands two and three, aspect and moisture appeared the most influential on oak site selection. In contrast, maple appeared most impacted by slope and canopy cover conditions.

The effect of the presence of the invasive exotic species autumn olive and honeysuckle on seedling relative density appeared most notably on maple (Figure 6). Relative densities of oak and maple seedlings were nearly equal in the absence of these two exotic woody species; however, in their presence, oak seedling relative density remained constant across all stands. In contrast, maple relative density decreased by nearly half when these exotic species were present in the measured stands, suggesting that maple, autumn olive, and honeysuckle compete in similar microhabitats during the earlier stages of forest stand establishment.

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 sufficient canopy openness needed to promote competitive oak regeneration (Moser et al. 2006; Hutchinson et al. 2008). The higher BA per ha in stand four 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 with other studies (Fralish et al. 1991; Fralish 1994; Abrams 2003; Ozier et al. 2006; Kabrick et al. 2008) and may explain variation among stands in relative abundance. The higher numbers of sugar maple in stand three 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; Brose 2010; 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 (Franklin et al. 1993; Bowles et al. 2005). 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 (fire, insect herbivory, etc.), facilitate an increase in mesic germination sites that favors further maple seedling establishment (Franklin et al. 2003; Kreye et al. 2013). 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; Kabrick et al. 2008).

Since successful oak regeneration has been linked to forest disturbance and lower stocking rates (Crow 1988; Abrams 2003; Bowles et al. 2005; Royse et al. 2010), oak seedling densities were predicted to 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 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 an advantage over oak seedlings and saplings that need direct sunlight throughout its life (Fralish 2004; Ozier et al. 2006; Nowacki and Abrams 2008; Thomas-Van Gundy et al. 2014). In addition, the positive effects of fire without canopy disturbance on oak regeneration may be short lived and not be sufficient to disrupt the successional trends towards shade tolerant species (Franklin et al. 2003; Abrams 2003; Royse et al. 2010; Nuttle et al. 2013; Kreye et al. 2013; Thomas-Van Gundy et al. 2014).

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). While oak is tolerant to 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 (Nigh, Pallardy, and Garrett 1985; Horsley et al. 2002; Kabrick et al. 2008). Most importantly, the environmental shifts generated by maple dominance in the canopy and subcanopy will specifically shift the understory environment towards microenvironments that favor maple seedlings (Kreye et al. 2013). In these forest stands, oak may be simply surviving in the microsites available as sugar maple alters environmental conditions that reduce disturbance and facilitate moister and cooler microsites, further reducing the ability of oak to recruit into the next size class (Nowacki and Abrams 2008; Kreye et al. 2013). The consistency of environmental preferences among stands further suggests that silvicultural treatments have not altered the underlying physiological constraints on tree regeneration.

Seedling responses in this system suggest there are different physiological mechanisms involved in regulating oak and maple regeneration. Maple species appear to be selectively recruiting into specific microhabitats. These sites 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 single thinning or fire prescriptions alone are insufficient to restrict maple to preferred environments (Kabrick et al. 2008; Thomas-Van Gundy et al. 2014). Several studies suggest using prescribed burns prior to and after group selection thinning which would promote oak seedling root development while culling current sugar maple regeneration (Crow 1988; Franklin et al. 1993; Delucia et al. 1998; Fralish 2004;

Haas and Heske 2005; Moser et al. 2006; Ruffner and Groninger 2006; Hutchinson et al. 2008). Other studies show successful oak regeneration in shelterwood cuts followed by a medium to high intensity spring prescribed burn (Brose 2010; Royse et al. 2010).

The effects of slope and aspect on patterns of maple and oak regeneration in this study supports the argument that landscape position could be used by land managers to pinpoint silvicultural treatments at the stand level. Because maples and other shade tolerants have shown the ability to stump sprout (Tift and Fajvan 1999; Hutchinson et al. 2008) and achieve sapling sizes resistant to fire, maples in the subcanopy should be both mechanically and chemically culled (Hutchinson et al. 2012; Kreye et al. 2013). 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. Exotic invasive autumn olive and bush honey suckle have been documented to reduce native tree seedling and sapling growth (Hartman and McCarthy 2007). Since observations in this study suggest autumn olive, honey suckle, and maple are competing in similar microhabitats, silviculture prescriptions aimed to reduce maple in areas of expected colonization may also effectively counter the establishment of woody exotic invasives. By effectively targeting management efforts, land managers may focus on those sites most likely to result in increased oak regeneration.

CONCLUSION

Results from the study suggest oak and maple seedlings do selectively recruit into specific microhabitats; however, the scale of microhabitat selectivity varies between communities at the stand scale. Although this study failed to show consistent silvicultural treatment effects on stand microhabitats, the constant separation between oak and maple seedlings across measured environmental variables advocates that stand level disturbances do play a role in habitat partitioning. Single event silvicultural prescriptions may not be effective at altering seedling-environment relationships. Future studies should be designed to measure the combined effects of both prescribed burns and controlled thinning on oak and maple establishment and regeneration.

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Table 1.—Description and history of the upland oak sites sampled.

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	5.6	Secondary-growth	Yes	No	27.9
5	17.99	Secondary-growth	No	No	31.8

Table 2.—Effects of landscape position on tree distribution in the understory and canopy forest layers. Results from a MANOVA test using Wilks' Lambda statistic. P-values in bold are significant.

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

Table 3.— Habitat specificity in maple and oak seedling relative to random points. Results from a MANOVA test using Wilks' Lambda statistic. P-values in bold are significant. Visualization of these data are presented in figure 4.

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

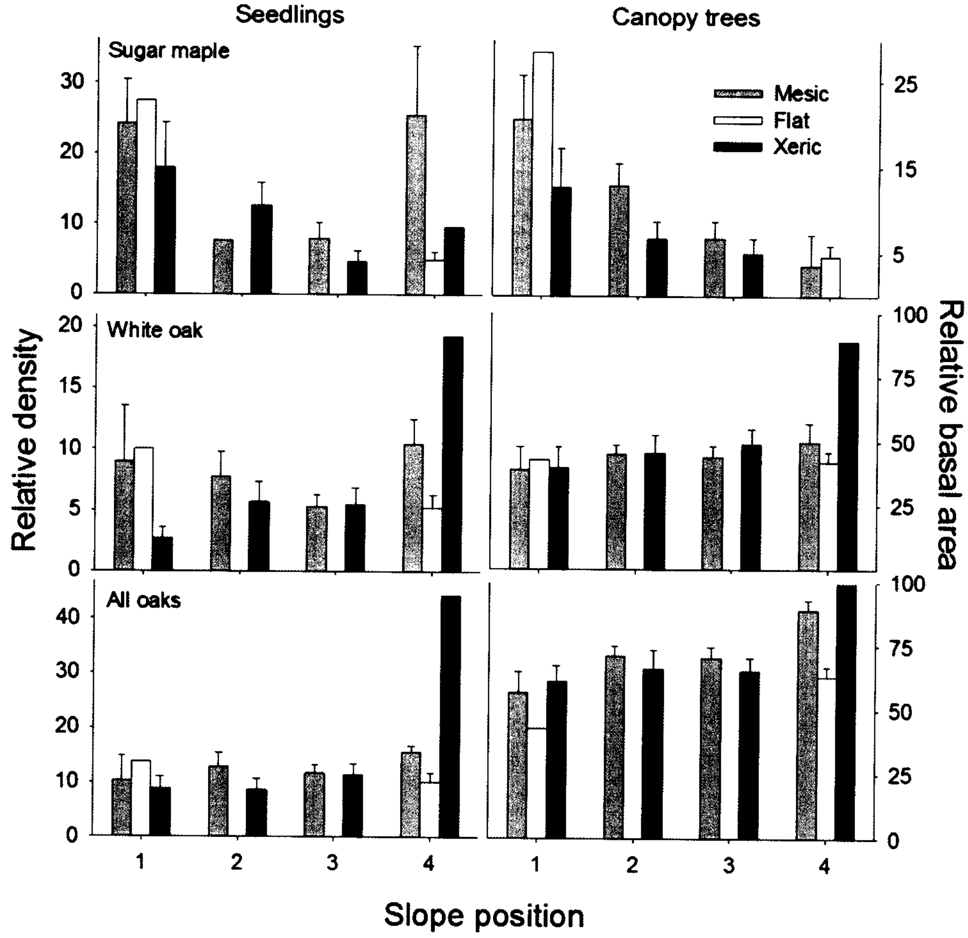

Figure 1.—Effect of slope position and aspect on the distribution of oak and maple in the forest understory and canopy. Slope position – 1: low, 2: mid, 3: high, 4: plateau. Patterns of relative abundance in the canopy followed trends commonly associated with upland hardwood forests. Sugar maple seedling 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. White oak and all oak seedlings combined were fairly uniform across all slope positions and aspects in the understory, similar to the overstory pattern. Sugar maple seedling's mirrored presence with oak seedling's suggest that sugar maple is expanding into areas traditionally dominated by oak regeneration.

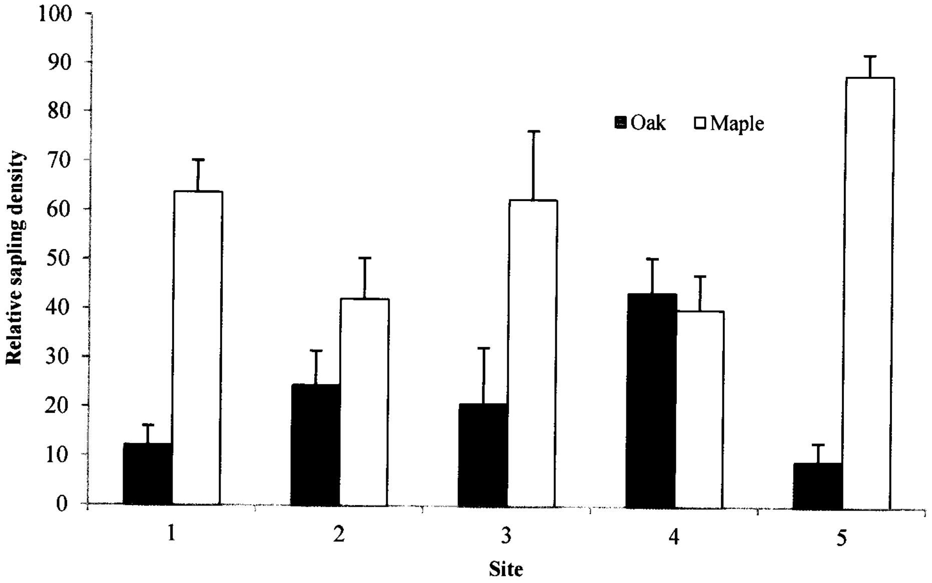

Figure 2.— Oak and maple sapling densities across study sites. 1: thinning, 2-4: prescribed burn, 5: no treatment. Maple relative sapling density was greater than oak at all sites, except in stand 4. However, the entire maple sapling population exceeded oak and outnumbered oak at 16 of the 43 sampled points in stand 4. This pattern suggests oak and maple species are separating along environmental gradients available at the stand level.

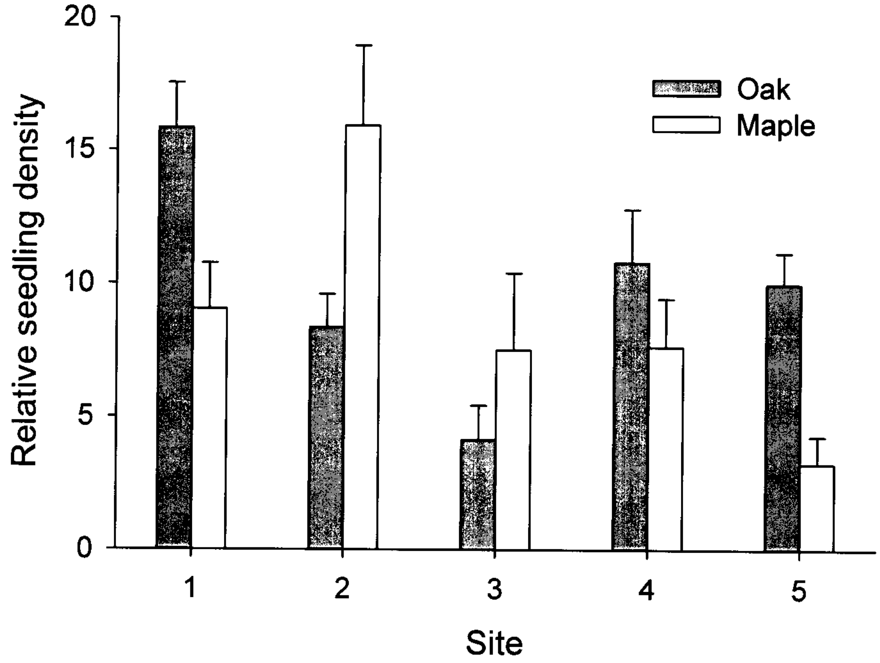

Figure 3.— Oak and maple seedling densities across study sites. 1: thinning, 2-4: prescribed burn, 5: no treatment. The single event prescribed burns without overstroy removal appeared not to disrupt the successional trend towards sugar maple in stands 2 and 3. The majority of the sampling locations in stand 3 were at either high or plateau slope locations, suggesting the area was more susceptible to adjacent seed sources of wind-blown maple seeds.

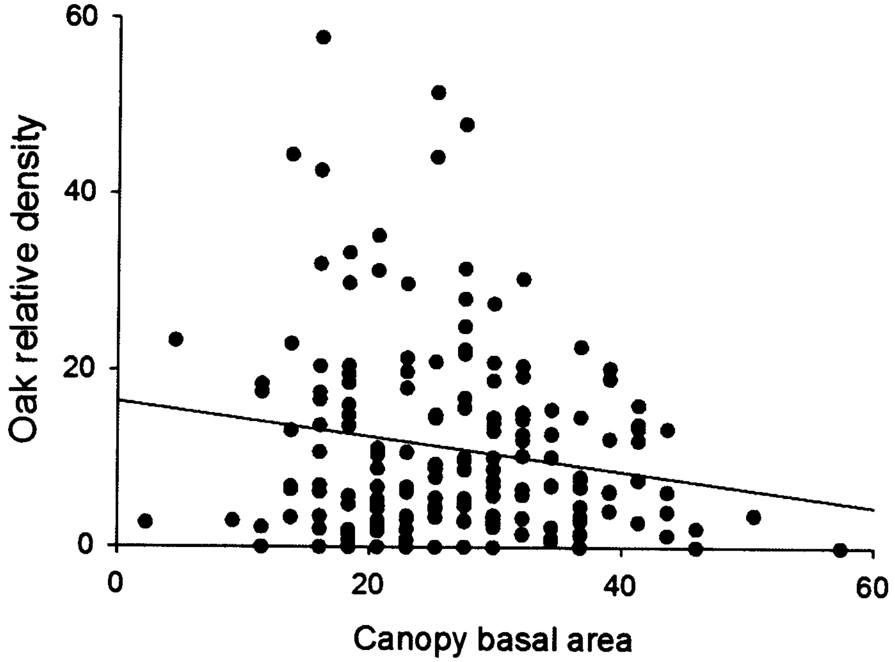

Figure 4.—Relative density of oak seedlings as a function of basal area of overstory trees using a Pearson correlation with 178 degrees of freedom. As expected, oak seedling densities increased as the BA per ha of overstory trees decreased. There was an overall significant negative correlation (R=-0.16, P=0.028) between canopy BA and oak seedling relative density. However, when the effect was analyzed separately for each stand, there was only a significant correlation in stand four.

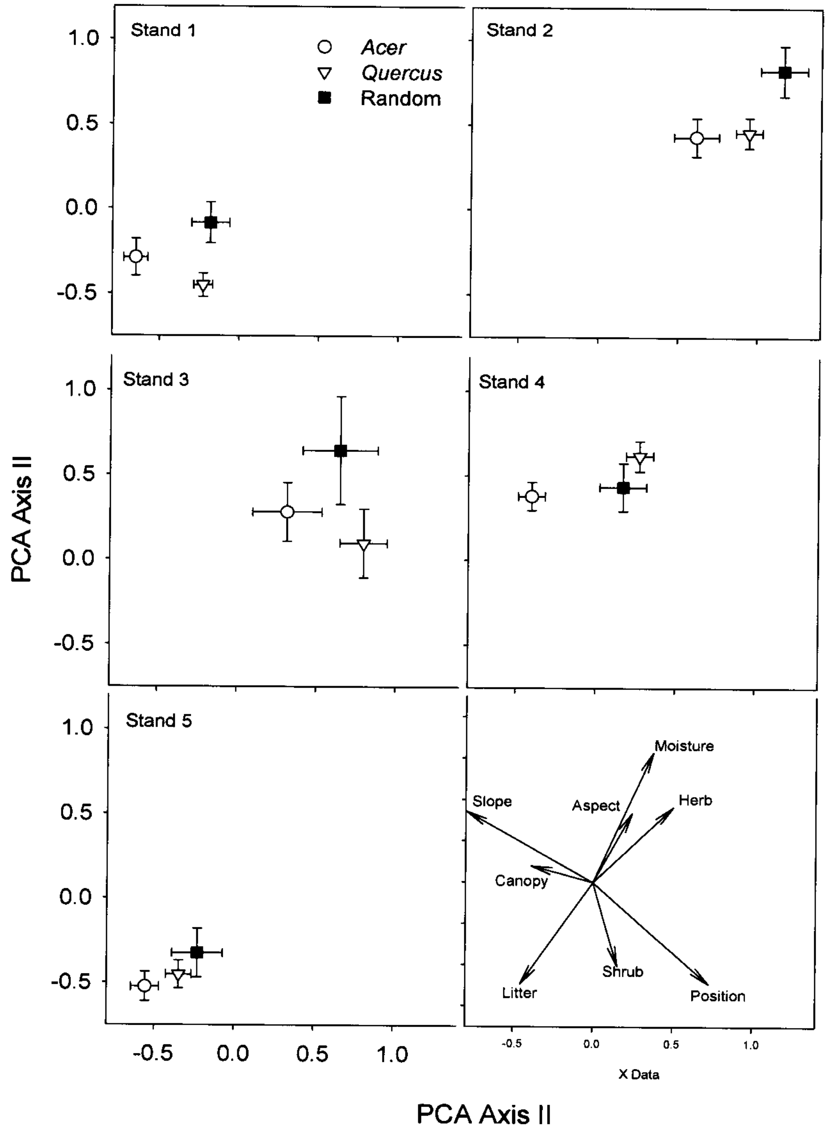

Figure 5.— Environmental selectivity of oak and maple seedlings in relation to random points. Data come from a PCA ordination of environmental variables. Lower right panel portrays the loading of each environmental variable on the PCA. The PCA of seedling and random microhabitats resulted in two informative axes (eigenvalues over 1) and explained 25.0% and 17.7% of the variation in the data set respectively. However, oak and maple seedlings were consistently separated from each other and from random points in each stand.

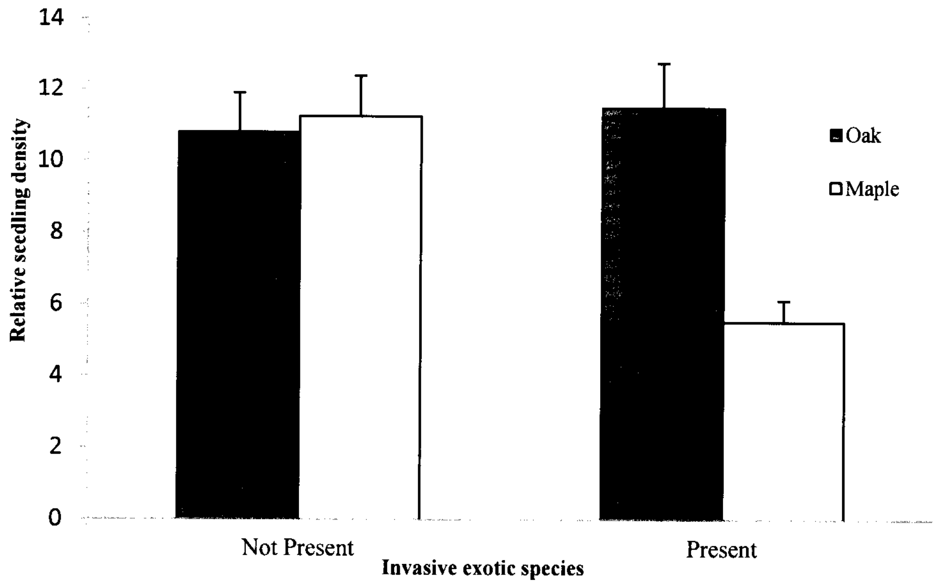

Figure 6.— Presence of invasive exotic species honeysuckle and autumn olive effect on relative oak and maple seedling densities across all stands. The reduction of maple relative density by nearly half when exotic species are present suggest that maple, autumn olive, and honeysuckle compete in similar microhabitats and can be co-targeted during silviculture prescriptions.