Adaptive Management for Urban Oak Ecosystem Restoration: Effects of Canopy Thinning on Seedling Regeneration and Groundlayer Plant Communities

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Adaptive Management for Urban Oak Ecosystem Restoration: Effects of Canopy Thinning on Seedling Regeneration and Groundlayer Plant Communities

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A Thesis
Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science At the University of Connecticut 2018
Adaptive Management for Urban Oak Ecosystem Restoration: Effects of Canopy Thinning on Seedling Regeneration and Groundlayer Plant Communities

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Acknowledgments

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Abstract

Oak forests are complex, fire dependent ecosystems, critical for supporting ecosystem services such as biodiversity and carbon storage. However, throughout eastern North America, previously oak-dominant ecosystems have undergone shifts in species composition and structure, primarily as a result of human influences. Land managers face the challenge of restoring oak ecosystems and promoting oak regeneration in urban and suburban natural areas, where high intensity silvicultural treatments are often not feasible. To investigate management alternatives, an adaptive management experiment was implemented in Lake County, IL in 2012, in which five thinning treatments of varying intensity, timing, and spatial aggregation were replicated across three study areas. I monitored the survival, growth, and morphology of planted oak seedlings and quantified microclimatic responses to the overstory thinning strategies. Understory light availability, soil temperature, and atmospheric temperature differed among treatments, suggesting that overstory thinning affected understory microclimates. Even though light availability was significantly increased by canopy thinning, survival and growth of planted oak seedlings did not differ among treatments. Overall high seedling survival rates suggest that current conditions in these sites are amenable to oak regeneration even with only subcanopy-focused management. However, further monitoring will be needed to assess the potential for canopy thinning treatments to influence transitions to the sapling and canopy layers. The results of this adaptive management experiment demonstrate a lower intensity alternative to traditional even-aged silvicultural methods that could be utilized for oak woodland management and restoration in urban ecosystems and natural areas throughout the eastern U.S.

Key Words: adaptive management; exurban development; oak ecosystem; regeneration; restoration; management; overstory thinning
Chapter 1

Response of under planted oak seedlings to restoration-focused canopy thinning in an urban oak ecosystem

Jillian Pastick

MS Thesis

For submission to Forest Ecology and Management
1 Introduction

Over the past 300 years, oak ecosystems in eastern North America have undergone dramatic shifts, transitioning from open canopied woodlands dominated by shade intolerant, xeric oak species, towards dense canopied forests with increased dominance of mesophytic species, such as sugar maple (*Acer saccharum*) (Dey, 2002, Nowacki and Abrams, 2008). These changes have been associated with a range of anthropogenic factors including fire suppression, shifts in disturbance regimes, acorn consumption by mammal populations (Knight et al., 2009, Marquis et al., 1976, Healy, 1997), and the spread of invasive plant and pest species (Nowacki & Abrams 2008, Abrams 1992). Another major issue is suburban and exurban development throughout the landscape (Fahey and Casali, 2017), which has accelerated and enhanced many of these anthropogenic stressors, especially by reducing the size and number of remnant forests.

The shift to dominance by mesophytic, shade tolerant species has increased canopy density, with negative consequences for oak regeneration (Dey and Kabrick, 2015, Larsen and Johnson, 1998). In many oak ecosystems, oak seedlings occur at relatively low densities and oak saplings and understory trees are exceedingly rare (Fahey et al., 2015, Dey et al., 2015, Abrams, 1992). For example, in Chicago, oak seedlings and saplings make up 1.6% and 0.3% of the understory respectively, a pattern evident throughout the Eastern region (Dey 2002, Maurer et al. 2013). Challenges with oak regeneration are often attributed to poor initial establishment and slow juvenile growth (Lorimer, 1993, Van Lear and Brose, 2002), with the latter often considered a more serious problem. In densely shaded stands, oak seedlings can establish, but do not develop into competitive seedlings and saplings (Dey, 2002). This oak regeneration bottleneck has raised concerns about the future sustainability of oak ecosystems throughout North America requires appropriate adaptive management strategies in order to encourage oak regeneration (Iverson et al., 2008). Sustainable management of these systems will depend on treatments informed by oak silvics, regeneration ecology, and understanding of the novel climate, disturbance and urban development stressors affecting these ecosystems (Dey, 2002).
Although browse, herbivory, disease and competition play an important role in the regeneration of oak species, studies suggest that light may be a limiting factor for the seedling-sapling transition (Dey, 2002). Light saturation of photosynthesis for oak seedlings occurs between 30 and 50% of full sunlight (Dey, 2002, Ashton and Berlyn, 1994, Wuenscher and Koslowski, 1971, Maurer et al., 2013), while growth in height and diameter of seedlings is greatest at about 50-70% of full sunlight (Hodges and Gardiner 1993, Gottschalk, 1994). Oaks experiencing low light levels that inhibit their growth typically increase allocation of carbon to above ground biomass, which can impede the development of roots and the growth of the plant (Gottschalk, 1987, Kolb and Steiner, 1990, Johnson et al., 2002, McShea and Healy, 2002). Initially, young oak seedlings have a relatively high shade tolerance, due to a large energy reserves in the acorns (Burns and Honkala, 1990), which can last well past germination. These energy reserves are dependent on the size and condition of the acorns (Bartlow et al., 2018). However, without adequate light, young seedlings can quickly die, which may lead to the bottleneck many oak ecosystems experience with seedling recruitment to the sapling stage (Lorimer, 2003). Under dense, closed canopies oak tolerance to shade is not great enough to compete with shade tolerant species. Therefore, management that creates more suitable understory light environments may encourage oak seedling regeneration, and improve the competitive balance between oaks and shade tolerant species, such as sugar maple.

Environmental conditions aside from light may also influence seedling survival and growth, including soil and atmospheric conditions. For oak species, soil temperature can play an integral role in seedling germination and growth in the early stages of regeneration (Johnson et al., 2002; Larson and Whitmore, 1970). Oak species, such as black and white oak, are much more efficient in their use of water than more shade tolerant species, like sugar maple, to a threshold leaf temperature of about 35°C (Wuenscher and Kozlowski, 1971, Johnson et al., 2002, McShea and Healy, 2002). Oak species are also more tolerant of drought conditions due to their leaf morphology and extensive root systems (Abrams, 1990, Dey, 2002). This suggests that increased atmospheric temperature and reduced soil moisture may improve oak seedling competitive ability relative to more shade tolerant species. However, this is only true within a particular range, as oak species still experience stress under extreme temperatures and very
low soil moisture conditions (Larsen and Johnson, 1998). Although these environmental characteristics are most important at early stages of seedling development, advantages conferred at that stage could be beneficial later in the transition from seedling to sapling and in competition with mesic species.

Active management may have some potential to prevent or reverse the transition of oak ecosystems to maple-dominated hardwood forests, especially through a combination of canopy manipulation and repeated fires (or application of fire-surrogate treatments). Although recommended management practices for oak ecosystems exist, they often rely on high intensity treatments and even-aged silvicultural systems (Lorimer, 2003, Dey, 2002). Such approaches may not always be feasible in natural areas or forests within densely populated urban and suburban areas. For this reason, a priority of ecological-focused silviculture should be to develop lower intensity management strategies for oak ecosystems that are socially acceptable to urban-exurban communities. Low intensity treatments such as sub-canopy thinning and cool season surface fires can encourage some regeneration, but can continue to favor shade tolerant species like beech and sugar maple (Dey, 2002). Targeted canopy thinning and gap creation may be able to both reduce the competition of shade-intolerant species as well as create beneficial microclimates (Latif & Blackburn, 2009) suitable for oak regeneration and diverse herbaceous communities in the understory. Canopy thinning alleviates stress of competition on planted oak seedlings (Dey et al. 2008), which would be advantageous for oaks at the earliest stages of regeneration.

Successful oak regeneration is generally dependent on adequate advance reproduction (Sander, 1971). For this reason, multiple interventions may be beneficial, with initial canopy opening allowing increased light in the understory to promote reproduction of oaks and development of an advanced regeneration layer, followed by heavier thinning to release advance regeneration of oak seedlings. This could be viewed as a shelterwood with reserves system. Such multi-cohort management techniques are likely to be an important tool in management for oaks in urban-exurban landscapes. For example, a shelterwood/burn method has been used for oak regeneration in the Piedmont of the southeastern United States, in which about 50% of basal area is removed, followed by a relatively hot prescribed burn approximately 3-5 years later (Brose and Van Lear, 2002). In areas where use of prescribed fires is
possible, such approaches might be an important component of the silvicultural system. Where fire is not possible or would limit early establishment of oak advance regeneration, fire surrogate treatments such as understory thinning and removal of invasive shrubs, may be highly beneficial.

Land managers and researchers are attempting many different strategies to restore oak ecosystem structure and function and promote oak regeneration (Maurer et al., 2013). My research focused on one example of a strategy attempting this in the context of urban-exurban natural areas management and the constraints placed on management options by an urban socio-ecological landscape setting. The Southern Des Plaines River Project in Lake County, Illinois is a long-term adaptive management experiment focused on restoration of oak ecosystem structure and function, meaning it is attempting to restore the role of the ecosystem within the landscape. The project focuses on testing novel multi-cohort forest management strategies as restoration actions, including a focus on phased, partial canopy removal (Maurer et al., 2013). A primary goal of the project has been to test low intensity silvicultural treatment options that could be applied in natural areas and forests across human-dominated landscapes. Canopy thinning strategies applied in the project vary in intensity, timing, and spatial pattern of removal, and have been overlaid on sites with a ~20-year history of low intensity prescribed fire and invasive species removal. Research on the broader project is focusing on a wide variety of ecological responses to treatments, including groundlayer plants, invertebrates, birds, canopy tree growth and carbon dynamics. In the study presented here, I focus on the effects of various canopy thinning treatments on oak regeneration and the potential for the treatments to promote development of an oak advance regeneration layer.

My overall goal was to assess the effect of canopy manipulation on planted oak seedling survival and growth and to relate seedling responses to environmental conditions. In order to understand this relationship, the study explored four specific objectives:

1. Assess seedling survival and growth in relation to thinning treatments
2. Characterize resource and microclimatic environments associated with thinning treatments
3. Evaluate relationships between environmental conditions and seedling survival and growth
4. Assess seedling traits and their relationship with survival and growth

By exploring these objectives, I hoped to gain a better understanding of the potential for successful oak seedling regeneration relative to different canopy thinning treatments, and determine which management methods are most appropriate for encouraging oak regeneration in urban and exurban landscapes.

2 Methods

2.1 Study Area and Sampling Methods

This study was conducted in the Southern Des Plaines River Adaptive Management Project (SDPR), which is arranged across three suburban natural areas (Ryerson Conservation Area, MacArthur Woods, and Elm Woods) in Riverwoods and Mettawa, Illinois, U.S., in the northern part of the Chicago metropolitan region. The SDPR is directed and maintained by the Lake County Forest Preserve District (LCFPD) and was initiated in 2011. Each of the sites is located along the east flank of the Des Plaines River and includes relatively large areas of contiguous, intensively managed dry-mesic oak forest. These forests are the most common type of upland forest in Illinois, with a more open canopy than typical mesic upland forests. Modern dry-mesic forests contain dense oak-maple dominated canopy, but were historically more open canopied (Fahey et al. 2014). Historically, the region was dominated by oaks, with white oak (Quercus alba) dominating the woodland and forest ecosystems of the area (Fahey et al. 2014), and red oak (Quercus rubra) and mesophytic species located in more fire-protected sites (Bowles and McBride 2005; Bowles et al. 1994). The climate of the area is continental, with average temperatures from -6 °C to 23 °C, experiencing humid summers and punctuated drought (Bowles et al. 2017). The SDPR is a long-term experiment that focuses on phased treatment implementation and adaptive management. In this study, I focus on impacts of the initial phase of canopy thinning treatments, which varied in intensity and spatial pattern.

2.2 Treatment Implementation
Appropriate dry-mesic study areas were located at each of the three sites and divided into 2-10 ha treatment units to which the five SDPR treatments were randomly assigned. However, treatment units were not the same size throughout the three sites. In all treatment units, sub-canopy thinning (80% removal of stems <20cm diameter at breast height; DBH) was conducted prior to canopy manipulation in winter 2011 and 2012. The five initial canopy (defined as stems ≥20cm DBH) thinning treatments included understory removal only (0% canopy basal area removed); light thinning treatment (10% canopy basal area removed); group shelterwood (aggregated removal of 17.5% of canopy basal area); moderate thinning (20% canopy basal area removed); woodland structure (40% canopy basal area removed; Fig. 1). Treatments were implemented in 2011 at MacArthur Woods in only 10 of 15 total treatment units (due to wet, snow-free ground conditions), with the remaining 5 units at that site and all the units at Elm Woods (10) and Ryerson Conservation Area (15) receiving treatments in 2012. Prior to treatment implementation three randomly located 0.1 ha circular monitoring plots (17.8 m radius) were established within each treatment unit in a randomized block design, totaling 120 plots. Ryerson Conservation Area and Macarthur Woods each contained three replicate treatment units, with three plots per treatment unit for each of the five treatments (45 total sample plots each), while the Elm Woods site only contained two replicate treatment units, with three plots per treatment units for each of the five treatments (30 total sample plots). Pre-treatment data were collected at each plot across all three sites in the summer of 201, including groundlayer percent cover (4-1m x 1m quadrats), shrub layer cover (5.64 m radius within the center of the 17.8 m radius plot), and diameter at breast height (DBH; 1.37m) for all trees >10 cm in DBH within the 17.8 m radius plot.

After treatment implementation (Spring 2012 and 2013) oak seedlings were planted in each plot. White oaks (Quercus alba) were planted at the center of each plot and at 5, 10, and 15 meters from plot center in each cardinal direction (13 total per plot; Fig. 1). A single red oak (Quercus rubra) and bur oak (Quercus macrocarpa) were planted at random directions within a 5-meter radius of plot center. Seedlings were grown from acorns collected in Lake County and were out planted at two years of age as
bare-root seedlings. Initial heights and diameter at base of the planted seedlings were recorded as baseline data. Seedling locations were marked with pin-flags, but seedlings were not individually tagged.

2.3 Light Availability

Photosynthetically active radiation (PAR) in the understory was measured using a ceptometer (AccuPAR PAR/LAI, LP-80, Decagon Devices) at 1 meter above ground in the center of each plot and 5, 10, and 15 meters in each cardinal direction, totaling 13 locations per plot. These locations were the same locations as the planted seedlings. Ten readings were taken 10 seconds apart from each other, and were averaged for each of the thirteen locations. Readings were taken once per plot from July to August of 2016 and May to August of 2017, between the hours of 8 am and 5 pm. Above canopy PAR readings were taken using Photon Flux Sensors (PAR Photon Flux Sensor, Decagon Devices) attached to a data logger (EM-50, Decagon Devices). The data logger and sensors were placed in an open field at each site and “above canopy” measurements were taken at 10 minute intervals. The transmitted PAR reaching the understory was calculated at the plot level by dividing understory PAR measurements by “above canopy” readings taken at the same time as the understory PAR measurements.

Hemispherical canopy photographs were used to estimate measures of light conditions in the understory, including canopy openness, leaf area index (LAI), and estimated percent of total above-canopy radiation transmitted (referred to hereafter as Gap Light Index or “GLI”; Canham, 1988). Five photos were taken at 1m above ground in each plot using a Nikon digital camera and fish eye lens, one in the center of the plot and 5 m in each cardinal direction, totaling 5 images per plot. In each photo, a compass was used to ensure the camera was facing north. A spirit bubble level was used to ensure the camera lens was level for the photograph. Images were analyzed using the Gap Light Analyzer (GLA) software (GLA, Cary Institute of Ecosystem Studies) (Settings for program in Appendix), and then averaged at the plot level. Photos were taken once per plot between July and August of 2016, and June and October of 2017 on full cloud days.

2.4 Additional Environmental Conditions
Additional environmental condition data were collected at one of the sites - Ryerson Conservation Area (selected due to ease of access). Soil percent volumetric water content (VWC) and soil temperature data were collected at the center of each plot and 5, 10, and 15 meters in each cardinal direction, totaling 13 measurements per plot using a soil moisture sensor (WET-2, Delta-T Devices). These measurements were then averaged at the plot level. Atmospheric temperature was also collected at the center of each plot. Forty-Five IBuytons (DS1920, Maxim Integrated) were attached to dowels located approximately 20 cm above the canopy floor. The IBuytons were covered with white bowls to reflect radiant energy. IBuytons captured temperature readings every thirty minutes for each day between June and August 2017. Maximum daily temperatures were obtained for each plot and were averaged by treatment to explore the most intense temperature conditions experienced within each plot.

2.5 Groundlayer Cover and Tree Cover

Data on groundlayer and shrub layers were collected both prior to treatment in 2011 and 5 years post-treatment in 2016 (30 plots at MacArthur) and 2017 (15 plots at MacArthur and all Elm and Ryerson plots). Data on percent cover of groundlayer plants were obtained in 4 - 1 x 1 m quadrats located 5 m from plot center in each cardinal direction in each plot. Stems for woody vegetation < 1 m in height were also counted in these quadrats and all stems of naturally regenerated oak seedlings were measured (diameter, height, approximate growth). We calculated percent cover averages and relative stem density of oak species by plot for pre-treatment and post-treatment monitoring. In the analysis, the groundlayer percent cover data were used as an additional environmental condition predictor variable, while the relative stem density of oak seedlings was analyzed as an explanatory variable. Shrub data were collected within a 5.64 m radius (0.001 hectare) subplot at the center of each plot. All living woody stems > 1 m in height and <10 cm in DBH were tallied into size classes (< 1 cm DBH, 1-5 cm DBH, 5-10 cm DBH). Species, DBH, cover class, azimuth, and distance were recorded for all trees >10 cm DBH on the full plot (17.8 m radius) we recorded species, DBH, cover class, azimuth, and distance. From these data, total plot basal area for both pre-treatment and post-treatment time periods were calculated.

2.6 Planted Seedling Survival & Growth
Planted oak seedling height (stretched length of the plant) and diameter at the base of the plant were measured on all living seedlings across all three sites, 5 years post-planting in 2016 and 2017. Average height, basal diameter, and basal area were calculated at the plot level for each of the 120 plots and compared to pre-treatment plot averages. Plot-level averages were used because seedlings were not individually tagged, thus post-treatment measurements could not be directly matched to seedling measurements in pre-treatment. The status of each planted oak seedling (alive or dead) was also recorded at the time seedling height and diameter measurements were taken at all plots across each of the three sites. Rates of seedling survival were calculated at the plot level as a percent of seedlings alive five years after planting.

2.7 Planted Seedling Leaf Characteristics

Additionally, at the Ryerson site only, seedling leaf area and estimates of leaf dry mass, leaf wet mass, Specific Leaf Area (SLA), Leaf Mass per Area (LMA), and percent C and N content were obtained for a subset of leaves from each of the living seedlings. To estimate leaf characteristics three leaves, including the petiole, were collected from the top portion of the seedling. Collected leaves were placed in a Ziploc bag between wet paper towels, placed in the refrigerator within 5 hours of collecting, and refrigerated between 24 and 48 hours. They were then brought to the lab, weighed, photographed against a white background containing a red square of 3 x 3 cm using an iPhone 6 (~20 cm from the leaf), and dried in a forced-air oven at 70 °C to a constant mass and weighed. At a later date, the leaves were homogenized using a ball grinder, rolled into aluminum tins, and run through an elemental analyzer (ECS4010, Costech Instrument) to obtain nitrogen and carbon content. Images of the leaves were then analyzed using the Easy Leaf Area program. A custom calibration was performed by creating a calibration file based on settings for 50 photographs. This file was then loaded and applied to the remaining leaves using autopilot mode.

2.8 Statistical Analysis

All statistics were performed on plot level averages of the data with treatment unit and site included as random effects, and results are presented as the mean value ± standard error (SE) of the five
treatments. Analyses were performed using R statistical software (Version 3.5.0). Analyses were run for all data for all three sites for seedling survival, growth, and environmental conditions. Because additional environmental and seedling characteristics data were collected for Ryerson, additional analysis was performed on Ryerson separately.

Variation in environmental conditions (Transmitted PAR, GLI, canopy openness, LAI, VWC, soil temperature, and maximum atmospheric temperature) and seedling characteristics (survival, height growth, diameter growth, basal area growth, % N content, % C content, LMA, SLA, and total leaf area) among the five treatments was analyzed using a linear mixed effects model with site and treatment included as random factors to account for spatial variation. I interpreted significant effects using ANOVA Type III on model coefficients. When main effects of treatment were significant, we performed post-hoc pairwise comparisons using difference of least means squares to compare model coefficients. All environmental conditions met the assumptions of normality except proportion of change in canopy basal area and GLI in the all site analysis and atmospheric temperature in the Ryerson site analysis. All seedling data met the assumptions of normality except for height growth and diameter at the base growth of the planted seedlings for the all site data, and C data for the Ryerson site analysis. In these cases, data were Log10 transformed to meet parametric and residual assumptions of the models.

Natural regeneration was assessed using mean values of change in relative stem density of oak species between pre- and post-treatment monitoring. A one-way ANOVA was used to evaluate differences among treatments. Additionally, we evaluated differences in relative stem density between treatments with pre-treatment numbers as a covariate by performing an ANCOVA in R.

Multiple regression in a model-selection framework was used to evaluate what ecological conditions and seedling traits most effectively explained seedling survival and growth. Sets of mixed-effects linear models that included all possible variations of the ecological variables were developed for the Ryerson Only and the All Site data sets. Additionally, for the Ryerson only data, models were created that included seedling traits as predictors of growth and survival for the Ryerson Only data. In both cases, several predictors (e.g., canopy openness and LAI) were highly correlated (Appendix II) and thus only
models that did not include combinations of strongly correlated \((r > 0.5)\) predictors were included in the final model evaluation set. All candidate models for Ryerson ecological condition models included Treatment Unit as a random effect, and all candidate models for All Site ecological conditions models included the interaction of treatment unit and site as a random effect. Linear effects models were analyzed using the lme4 package in R. Model fit was analyzed using Akaike Information Criterion (AIC) and AIC weights. All models were ranked by AIC and the models considered to be highly supported by the data were those with \(\Delta AIC < 2\) in relation to the most highly ranked model. Though model selection was conducted using comparisons of AIC scores, the goodness of fit of highly-ranked models was assessed as well. To assess the suitability of these models, \(R^2\) values and coefficients were calculated using the piecewiseSEM package in R.

3 Results

3.1 Environmental Conditions

Treatments differed in post-treatment canopy basal area \((F_{4,112} = 3.794, p = 0.006; \text{Fig. 2A})\) and proportion change in basal area from pre- to post-treatment conditions \((F_{4,113} = 3.666, p = 0.007; \text{Fig. 2B})\) and largely followed expectations related to intensity of thinning treatments. A pairwise comparison test revealed that the understory removal \((p = 0.003)\), light thinning \((p = 0.008)\) and moderate thinning \((p = 0.04)\) treatments had significantly higher post-treatment mean basal area than the woodland treatment. Change in canopy basal area did not differ among the treatments experiencing overstory removal, but was different between the understory removal only treatment and the four overstory removal treatments (Fig. 2B).

There was a significant difference in the mean transmitted PAR reaching the understory at 1 meter above the forest floor between the five treatments \((F_{4,110} = 9.043, p < 0.005; \text{Fig. 2C})\). As expected, transmitted PAR largely increased with increasing intensity of thinning treatments, with the lowest occurring in the understory removal treatments and the highest in the Woodland treatments. Mean gap light index also differed among treatments \((F_{4,108} = 7.986, p < 0.005; \text{Fig. 2D})\). There was a subtle
increasing trend with treatment intensity, with the lowest intensity treatment, understory removal only, having the lowest mean percent total transmittance (24.60%), and the highest intensity thinning, woodland, having the highest percent light transmittance (32.47%) (Table 1). Pairwise comparison suggests understory removal treatments had a significantly smaller mean percent total transmittance than group shelterwood plots (p = 0.003), light thinning plots (p = 0.040), and woodland plots (p < 0.0001). Moderate thinning plots also had significantly smaller mean total transmittance than woodland thinning treatments.

Additional environmental conditions were analyzed for the Ryerson site. Volumetric water content (VWC) was not significantly different among treatments (F_{4,38} = 2.297, p = 0.074), although soil temperatures were not found to be significantly different among the treatments (F_{4,38} = 2.270, p = 0.110; Fig. 3B). There did appear to be significant differences in mean maximum atmospheric temperature among the treatments (F_{4,38} = 5.910, p < 0.005; Fig. 3C), with an increasing trend in atmospheric temperatures with increasing intensity of thinning. Specifically, woodland plots had a significantly higher mean max temperature than light thinning plots (p = 0.002), group shelterwood plots (p = 0.008) and understory removal only plots (p = 0.001). Moderate thinning treatments also had a significantly higher mean maximum atmospheric temperature (p=0.009). There appeared to be an increasing trend, with max atmospheric temperatures increasing with increasing intensity of thinning.

### 3.2 Planted Seedling Survival and Growth

After 5 years, overall seedling survival was not significantly different among the five treatments or the three sites (F_{4,109} = 0.456, p = 0.768; Fig 4A). There was also no clear trend in the survival of seedlings based on the intensity of thinning (Table 2). Mean growth in seedling height ranged from 19.9 cm in the understory removal treatment to 29.2 cm in the group shelterwood treatment (Table 2), but did not differ significantly among the treatments (F_{4,107} = 1.263, p = 300; Fig. 4B). There was no significant difference in diameter growth among the treatments (F_{4,107} = 0.802, p = 0.531; Fig. 4C). Basal area growth was also not significantly different among the treatments (F_{4,106} = 0.967, p = 0.437; Fig. 4D), and
there were no obvious trends in the means, where basal area growth for all plots ranged from 0.0054 to 0.0083 cm$^2$ (Fig. 4D, Table 2).

### 3.3 Leaf Traits

Five years after oaks were planted, seedlings at Ryerson did not have significantly different mean leaf area ($F_{4,38} = 0.452$, $P = 0.770$; Fig. 5A) or total leaf area ($F_{4,38} = 3.248$, $p = 0.071$) among treatments. Mean leaf area ranged from 18.21 cm$^2$ to 19.59 cm$^2$ and mean total leaf area ranged from 585 cm$^2$ to 690 cm$^2$ (Table 2), demonstrating a great deal of variance within the treatments. However, planted seedling LMA was significantly different among the treatments ($F_{4,37} = 3.005$, $p = 0.042$; Fig. 5B). Post hoc analysis suggested that Woodland plots (0.020 mg/m$^2$) had a significantly higher mean LMA than both understory removal plots (0.017 mg/m$^2$, $p = 0.015$) and moderate thinning plots (0.017 mg/m$^2$, $P = 0.007$) (Table 2). SLA of planted oak seedlings also differed between treatments ($F_{4,35} = 4.464$, $p = 0.014$; Fig. 5C). Both understory removal (62.5 cm$^2$/g, $p = 0.010$) and moderate thinning (61.5 cm$^2$/g, $p = 0.024$) plots had significantly larger mean SLA than the woodland plots (51.9 cm$^2$/g) and group shelterwood plots (54.2 cm$^2$/g) (Table 2).

Seedlings differed in leaf % N content, but not in leaf % C content. Mean leaf N content (%) was significantly different among the treatments ($F_{4,37} = 2.688$, $p = 0.071$; Fig. 5D). Post hoc analysis suggested that light thinning mean N content was significantly higher than woodland thinned plots ($p = 0.016$) (Table 2). Mean leaf C content (%) was similar in all treatments, ranging from 47.4% to 47.9% ($F_{4,36} = 1.729$, $p = 0.161$) (Table 2; Fig. 5E).

### 3.4 Natural Oak Regeneration

Change in relative stem density of naturally regenerated oak seedlings did not differ significantly among the treatments five years after management implementation ($F_{4,38} = 0.407$, $p = 0.802$; Fig. 6). However, there was a slight trend of increasing mean relative stem density with increasing intensity of thinning (Appendix IV). Understory removal only (-39.96%) and group shelterwood (-24.8%) treatments both had negative mean percent change in relative stem density of oak seedlings, while relative stem density increased by 12.3% in the light thinning, 34.3% in moderate thinning, and 34.9% in woodland
treatments (Appendix IV). In the ANCOVA model, post-treatment relative stem density of oaks was modeled as the dependent variable with treatment as the factor and pre-treatment relative stem density as the covariate. The results indicated that post treatment relative density of natural oak seedling regeneration was strongly related to pre-treatment density ($F_{4,38} = 0.740, p = 0.007$). When pre-treatment relative stem density was included as a covariate, there was no significant difference in the post-treatment relative stem-density among treatments ($F_{4,38} = 0.591, p = 0.670$).

3.5 Predictors of Seedling Survival and Growth

All Sites Seedling Survival and Growth

Multiple regression models of planted white oak seedling survival with the highest levels of support included the variables gap light index (GLI), canopy basal area, change in basal area, and percent cover of groundlayer as predictors (Table 3). There were four top models within 2 ΔAIC units which together accounted for > 99% of the weight in the model set. All four models contained GLI and percent groundlayer cover and differed in the inclusion of change in canopy cover and canopy basal area. The null model had very little support relative to the model set as a whole ($ΔAIC = 109.10, w < 0.001$). The most highly supported model only included GLI and percent groundlayer cover as predictors (Table 3). This model had the highest weighting ($w = 0.37$) relative to the other top models ($w = 0.31, w = 0.18, w = 0.14$); and similar predictive power ($R^2 = 0.55$) to the other top models that included additional predictors (all $R^2 = 0.55-0.56$; Table 3). In this top model, survival increased with greater GLI and lower % groundlayer cover.

Multiple regression models of seedling height growth with the highest levels of support again included GLI, canopy basal area, change in basal area, and percent cover of groundlayer as predictors (Table 3). For height growth, there were three top models within 2 ΔAIC units which accounted for > 88% of the weight in the total model set. Similar to the model set for seedling survival, these models differed in the inclusion of two of the predictor variables, change in canopy cover and canopy basal area. The null model had very little support relative to the model set as a whole ($ΔAIC = 96.52, w < 0.001$). Seedling height growth was most strongly related to GLI, change in basal area, and percent cover of
groundlayer, although all models contained GLI and percent cover of groundlayer. Each variable in the top model had weak, indirect relationship with the height growth of seedlings. This means that as light increases, both seedling growth and groundlayer cover also increase. The top model had a much higher weighting \(w = 0.47\) relative to the other top models \(w = 0.22, w = 0.19\); however, it did not have especially stronger predictive power \(R^2 = 0.43\) relative to the other top models \(R^2 = 0.41 \& 0.42\; \text{Table 3}\).

Multiple regression models of seedling diameter base growth had the same top predictor variables found in both of the previous sets, GLI, change basal area, canopy basal area, and percent cover of groundlayer. The three top models within 2 \(\Delta\text{AIC}\) units contained the same combination of predictor variables as the seedling survival model set, and accounted for >77% of the weight of the set. Once again, the null model had very little support relative to the model as a whole \(\Delta\text{AIC} = 7.68, w < 0.006\). The most highly supported model indicated that seedling diameter growth was related to GLI and percent cover of groundlayer as the top two predictor variables. This model had a higher weighting \(w = 0.29\) than the other two models \(w = 0.20, w = 0.14\). However, in this model set, the top model with the highest weight also has the lowest predictive power \(R^2 = 0.24\) relative to the other two models in the set \(R^2 = 0.27 \& R^2 = 0.26\). Even though this relationship was relatively weak, GLI and percent cover of the groundlayer both demonstrated a positive relationship with diameter growth.

Marginal \(R^2\) values explain the fit of the fixed effects in the model, while conditional \(R^2\) values explain the fit of the model including the random effects. In all cases, the conditional \(R^2\) values were much higher than the marginal \(R^2\), which suggests that the random effect of treatment unit nested within site (Site: TU) was necessary within the model. In all model sets, every top model included GLI and percent cover of groundlayer.

*Ryerson Seedling Survival and Growth*

At the Ryerson site only, predictor variables did not explain much variability in the seedling survival and growth (Appendix IV). All top models had relatively low predictive power, with the diameter growth model set having the lowest predictive powers. Additionally, all top models had low
weight in the model sets \((w < 0.06)\). However, seedling survival and growth response to measured seedling traits demonstrated some predictive relationships. For seedling survival at Ryerson, leaf dry mass, leaf mass per area, mean seedling leaf area, and N content were the best predictive variables for seedling survival. The model with the highest level of support had an especially high weighting relative to the other models \((w = 0.91)\), but relatively low predictive power \((R^2 = 0.17)\). The null model had very little support relative to the other models in the seedling survival model set \((\Delta AIC = 29.58, w < 0.001)\). For seedling height growth, the top predictive variables were leaf dry mass and LMA, with two top models within 2 \(\Delta AIC\) units. The top model had a much higher weighting (dry mass) \((w = 0.434)\) relative to the other top model (dry mass and LMA) \((w = 0.16)\). However, not even the top model had strong predictive power \((R^2 = 0.12; \text{Table 4})\). Lastly, the diameter growth of seedlings at Ryerson was best explained by three predictors, dry mass of leaves, percent nitrogen content of leaves, and leaf mass per area. This model accounted for 53\% of the weight of the model set. Of the seedling trait models, predictive power was the highest for this model \((R^2 = 0.31)\). In all top models, for seedling survival and growth, dry mass was a top predictive variable. However, the predictive models for survival and height growth were relatively low. Additionally, the conditional \(R^2\) and marginal \(R^2\) values are comparable, which suggests that the random effect “treatment unit” does not greatly improve the predictive power of the variables within these top models.

4 Discussion

Light transmission to the understory as influenced by canopy structure is an easily manipulated variable to address management goals (Weiss et al., 1991), and promotes the success of oak regeneration (Larsen and Johnson, 2008, Dey et al., 2008). My data show that the low intensity canopy removal treatments applied in the SDPR project successfully increased light availability relative to areas that only received sub-canopy tree removals (18-28\% vs. 11\% of above canopy PAR transmitted). There were also significant differences among the canopy removal treatments, which generally aligned with the intensity of the treatment in terms of total basal area removal. With increasing intensity of thinning, proportion of
transmitted PAR, canopy openness and GLI also increased. Approximately 23% of plots undergoing overstory treatments had a transmitted PAR greater than 30%, which is the minimum often cited for oak survival (Dey, 2002, Wuenscher and Koslowski, 1971, Maurer et al., 2013). However, only 8% of plots reached the 50% light availability threshold, which is cited as being the lower limit for high growth rates in oak seedlings (Dey, 2002). In comparison, 0% of plots in the sub-canopy-only treatments reached the 30% threshold. Similarly, 31% of plots undergoing canopy thinning reached 30% GLI, but less than 1% exhibited greater than 50% GLI. This suggests that overstory thinned plots may be closer to the 50% threshold in proportion of transmitted PAR, but not as close in terms of gap light intercept. Shifts in the light environment were strongly related to canopy tree removal, however light in the understory can also be influenced by shrubs and groundlayer plants (Montgomery, 2004). Due to response of the shrub and herbaceous layer, canopy removal does not always have a strong direct effect on light availability in the ground layer (Kern et al., 2006), which could have affected the strength of the differences in light availability among the treatments. Groundlayer cover increased greatly in all treatments, but was higher in the overstory removal treatments than the understory only treatment, which likely affected light availability on the forest floor (and the potential for differences among treatments) to some degree. Overall, our results suggest that understory removal alone is not sufficient to alter the sub-canopy light environment, but also indicate that low intensity canopy removals may not be vastly superior in this regard (only increasing light availability by 7-17%), and may not create the open canopy conditions often associated with successful oak regeneration (i.e., 30-50% light availability; Dey, 2002).

One key to sustainable oak regeneration is encouraging both oak seedling survival and growth in the understory (Miller et al., 2017), which promotes development of an advance regeneration layer and eventual recruitment of seedlings into the sapling and canopy layer. In this study, seedling survival and growth did not differ among treatments, despite differences in the sub-canopy light environment which is often a limiting factor for oak regeneration (Parker and Dey, 2008, Giuggiola et al., 2015). Although there was no difference among treatments in survival of these small, 2-year-old seedlings, the overall survival rate for all treatments was approximately 45%. Across all treatments (including subcanopy removal only)
52% of plots had >50% of seedlings survive and 13% of plots had >75% of seedlings survive. These results suggest that conditions in these sites (across all treatments) over the 5-year period following the treatment were amenable to oak seedling survival. Growth of planted seedlings, both in terms of height and diameter growth, also did not vary significantly among treatments. However, rather than being high across all treatments, average seedling growth was lower than that exhibited in many studies of white oak (Berg, 2004). Even in the most heavily disturbed sites (the “Woodland” treatments), where percent PAR reaching the understory commonly reached >30%, rates of growth remained relatively low, contradicting what we expect for seedling growth. There were some statistically significant differences in leaf traits (N content, SLA, and LMA) among treatments that coincide with differences in light availability. Differences in leaf morphology matched expectations; when light levels are low, seedlings increase leaf area to collect more photosynthetically active radiation, therefore increasing SLA and decreasing LMA (Hoffman et al., 2005, Nesrine et al., 2014). N content was also higher at low light levels, which can be expected, as % N and SLA are typically positively correlated in deciduous plant species (Falxa-Raymond et al., 2012). It is possible for SLA and LMA to provide insight into photosynthetic productivity and capability of the seedlings (Poorter et al., 2009, Enrique de la Riva et al., 2016), however, in my study, differences in leaf traits were not especially strong and most likely not biologically meaningful, despite statistical significance of treatment differences.

Although survival of planted seedlings in the treatment areas was relatively high, canopy removal and associated increased understory light availability did not appear to encourage natural oak regeneration. There was not a consistent positive trend in relative density of natural oak seedlings, and there was also a lack of difference among treatments in the response of the natural regeneration layer (Fig. 6). This result would appear to correspond with results seen for planted seedlings, in that survival was generally high and similar across treatments. These results could also reflect a lack of any stimulation of additional oak seedling regeneration related to the treatments. However, seedlings were not tagged and so mortality and ingrowth patterns are unknown. Absolute density of oak seedlings was also not significantly different among treatments. Group-shelterwood plots demonstrated an increase in oak stem
density, as did the understory removal treatment. However, light thinning, moderate thinning, and woodland treatments did not experience an increase in stem density, and may have decline due to mortality that was related to the treatments or other factors. The lack of difference in relative stem density is most likely due to a combination of the decrease in absolute density and an increase in density of other woody species. Although these results may reflect the lack of a treatment influence on natural regeneration, it is also likely that the natural regeneration response is related to seedling browse, acorn consumption and lack of mast years, or competition with understory species for newly available light resources (Aldrich et al., 2005, Dey and Kabrick, 2015).

Canopy tree removal and changes to light availability can also impact abiotic factors in the understory, such as air temperature, soil temperature, decomposition, and soil weathering (Chen and Franklin, 1997, Silbernagel and Moeur, 2001). This influence of light on environmental conditions and abiotic factors was apparent at Ryerson, but not necessarily in the ways that would have been expected. Soil temperatures differed between treatments, but understory removal only plots had significantly higher soil temperatures than moderate thinning plots and group shelterwood plots, which was somewhat unexpected. One possible explanation is that the increased groundlayer cover shaded the soil, absorbing solar radiation and avoiding soil heating. Atmospheric temperatures followed a similar trend to the light environment, increasing with increasing intensity of thinning. However, where soil moisture was expected to be drastically influenced due to canopy tree removal and increased light availability, there was no significant difference. It is possible that this is because of the balance of decreased transpiration demand related to tree removal and increase light related evapotranspiration (Iverson et al., 2004). It is also possible that VWC was not measured frequently enough to capture dynamic soil moisture conditions. Micro-environmental conditions can be highly influential on seedling development (Kaelke et al., 2001), but I did not see a strong relationship between the measured microenvironment and oak seedling growth or survival. I did not measure every environmental condition associated with seedling survival, and as a result, there are likely to be other environmental factors that could be influential to seedling survival and
growth. For instance, nutrient availability in the soil can have a strong impact on seedling survival and growth (Devine et al., 2007).

Although resource availability and microclimatic conditions in the understory are often the primary drivers of seedling survival and growth, there are many additional factors that affect seedling success and could have impacted the potential for significant treatment effects in this study. Young seedlings can be influenced by a number of abiotic and biotic influences at this stage in seedling development, including drought, flooding, herbivory, and soil nutrient availability (Larsen and Johnson, 1998, Kaelke et al. 2001). It is possible that other local factors that were unmeasured had a greater impact on the seedlings (Knoot et al., 2010). For example, browsing damage is a common biotic factor that influences seedlings in their first five years of growth and establishment (Russell et al., 2001). Seedling monitoring indicated that around 15% of live seedlings demonstrated signs of animal browse (data not shown), and some component of seedling mortality was likely related to browsing damage.

Additionally, because the thinning treatments were meant as a low intensity alternative to traditional silvicultural approaches, they were not drastically different from each other in their effects on the understory growing environment. It is possible that there were no obvious differences between seedling survival, growth and morphology due to the lack of extreme differences between implemented treatments, even though these treatments had some statistically significant differences. For example, even in the spatially aggregated group shelterwood treatment canopy openings may not have been large enough and may not have provided enough light to increase white oak growth to a competitive level (Brose and Rebbeck, 2017). On the other hand, ubiquitous groundlayer competition associated with the treatments may have been intense enough to override the treatment effect. Groundlayer vegetation often presents issues of competition, limiting the newly available resources from being accessible to young oak seedlings (Dey et al., 2008).

The overall survival rate for planted seedlings was high, suggesting that low intensity canopy removal treatments were somewhat successful in encouraging oak regeneration. These results suggest that high intensity or even-aged methods may not be necessary to promote the development of an advance
regeneration layer in oak forests and woodlands where under planting is a possibility. These findings are especially important in natural areas and in exurban landscapes where land managers have limited silvicultural options. This research provides a basis for adaptive management strategies focused on urban oak ecosystems, where managers may be able to utilize low intensity canopy removals as an initial treatment in an adaptive management program, paired with planting and more intensive understory management in years following thinning implementation (Albrecht and McCarthy, 2006, Iverson and Hutchinson, 2008). Prescribed burning following the first thinning would be beneficial to the regeneration of white oaks (Albrecht and McCarthy, 2006, Larsen and Johnson 1998) by removing some groundlayer competition, and creating a more open sub canopy for seedling growth and development. This could then be followed by under planting of a substantial number of oak seedlings or broadcast seeding of acorns to allow development of a robust advance regeneration layer. Alternatively, treatments could be timed to coincide with mast years, although such flexibility may rarely be possible in practice (Maurer et al., 2014, Miller et al., 2017). Other management suggestions include exclusion fencing or seedling protection to reduce browse, and herbicide application or mechanical removal of groundlayer vegetation (especially woody invasive species) to reduce competition (Dey et al., 2008, Maurer et al., 2013).

Adaptive management strategies are most successful when they are consistent with current silvicultural and ecological literature relating to the outcome (Baker et al., 2017), with a set clear of measurable objectives, taking the conditions of the entire ecosystem into consideration. This study was designed in a way that allowed an experimental approach, comparing how different treatments influence regeneration, with the understanding that continued monitoring would influence subsequent management after the first 5-6 years. Continued monitoring is necessary to determine how current thinning has influenced the long-term regeneration and establishment of both planted and naturally regenerated oaks, and to determine what additional management is necessary to optimize oak regeneration. The growth of the seedlings planted in this study into the sapling layer is an important step in the development of a potentially viable advance regeneration layer (Brose and Rebbeck 2017). However, the “bottleneck” in oak regeneration is often the accession of oak saplings into the canopy layer (Lorimer, 1993), and longer-
term monitoring will be needed to evaluate this essential transition. Additional research and monitoring could also include more quantitative measures of deer browse and additional measures of seedling response to newly available sunlight in the form of photosynthetic capacity. These results will serve as the basis for future management decisions at these particular sites in the Chicago region, but can also be used to inform recommendations for oak regeneration strategies in urban and exurban oak ecosystems more broadly.
Figure 1

Treatment layout at one of the three study sites, MacArthur Woods. Each polygon represents a treatment unit and each color corresponds to a specific treatment: red is understory removal, light blue is light thinning, medium blue is moderate thinning, dark blue is woodland thinning, and red with green circles is group shelterwood. Yellow points within the treatment units represent a plot. In the bottom, left corner of the map is a diagram displaying the placement of planted seedlings throughout each of these plots. Each plot contained thirteen planted 13 white oaks (*Quercus alba*) – white symbol, one bur oak (*Quercus macrocarpa*) – yellow symbol, and one red oak (*Quercus rubra*) – red symbol.
Table 2

Mean values and standard errors of environmental conditions by treatment across all three study sites. Pre-treatment data is provided if available.

### All Sites Environmental Condition Means

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre or Post % Change</th>
<th>Understory Removal</th>
<th>Light Thinning</th>
<th>Group Shelterwood</th>
<th>Moderate Thinning</th>
<th>Woodland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open sky (%)</td>
<td>Post</td>
<td>17.4 ± 0.3</td>
<td>19.8 ± 0.5</td>
<td>20.2 ± 0.7</td>
<td>19.3 ± 0.4</td>
<td>22.2 ± 0.7</td>
</tr>
<tr>
<td>Total Transmission (%)</td>
<td>Post</td>
<td>24.6 ± 0.6</td>
<td>28.8 ± 1.0</td>
<td>29.5 ± 1.2</td>
<td>27.6 ± 0.9</td>
<td>32.5 ± 1.4</td>
</tr>
<tr>
<td>Leaf Area Index (m² / m²)</td>
<td>Post</td>
<td>1.86 ± 0.02</td>
<td>1.68 ± 0.03</td>
<td>1.64 ± 0.05</td>
<td>1.74 ± 0.03</td>
<td>1.55 ± 0.04</td>
</tr>
<tr>
<td>Transmitted PAR (%)</td>
<td>Post</td>
<td>0.11 ± 0.01</td>
<td>0.18 ± 0.02</td>
<td>0.23 ± 0.03</td>
<td>0.23 ± 0.02</td>
<td>0.28 ± 0.03</td>
</tr>
</tbody>
</table>

### Ryerson Environmental Condition Means

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre or Post % Change</th>
<th>Understory Removal</th>
<th>Light Thinning</th>
<th>Group Shelterwood</th>
<th>Moderate Thinning</th>
<th>Woodland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max Plot Temperatures (°C)</td>
<td>Post</td>
<td>36.9 ± 0.7</td>
<td>39.2 ± 1.5</td>
<td>40.0 ± 1.1</td>
<td>41.3 ± 1.2</td>
<td>44.9 ± 1.8</td>
</tr>
<tr>
<td>Volumetric Water Content (%)</td>
<td>Post</td>
<td>26.7 ± 1.5</td>
<td>29.4 ± 2.7</td>
<td>31.3 ± 0.9</td>
<td>25.6 ± 1.0</td>
<td>28.4 ± 0.9</td>
</tr>
<tr>
<td>Soil Temperature (°C)</td>
<td>Post</td>
<td>24.4 ± 0.2</td>
<td>22.9 ± 0.4</td>
<td>22.7 ± 0.6</td>
<td>22.0 ± 0.5</td>
<td>23.5 ± 0.3</td>
</tr>
</tbody>
</table>

### All Site Stand Structure Means

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre or Post % Change</th>
<th>Understory Removal</th>
<th>Light Thinning</th>
<th>Group Shelterwood</th>
<th>Moderate Thinning</th>
<th>Woodland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree Basal Area, m²/ha³ (Trees ≥ 10 cm DBH)</td>
<td>Pre</td>
<td>28.3 ± 1.3</td>
<td>30.5 ± 1.4</td>
<td>28.4 ± 1.2</td>
<td>30.6 ± 1.3</td>
<td>28.4 ± 1.8</td>
</tr>
<tr>
<td>% Change</td>
<td>Post</td>
<td>28.0 ± 1.3</td>
<td>26.2 ± 1.3</td>
<td>23.7 ± 1.5</td>
<td>25.1 ± 1.3</td>
<td>22.4 ± 1.8</td>
</tr>
<tr>
<td>Diameter Breast Height, cm² (Trees ≥ 10 cm DBH)</td>
<td>Pre</td>
<td>27.1 ± 1.0</td>
<td>29.4 ± 1.0</td>
<td>27.5 ± 0.9</td>
<td>30.8 ± 0.9</td>
<td>26.9 ± 1.0</td>
</tr>
<tr>
<td>% Change</td>
<td>Post</td>
<td>35.6 ± 0.6</td>
<td>39.5 ± 0.6</td>
<td>36.8 ± 0.6</td>
<td>38.9 ± 0.7</td>
<td>36.2 ± 0.6</td>
</tr>
<tr>
<td>Quadratic Mean Diameter, cm² (Trees ≥ 10 cm DBH)</td>
<td>Pre</td>
<td>32.1</td>
<td>34.4</td>
<td>32.8</td>
<td>35.9</td>
<td>31.8</td>
</tr>
<tr>
<td>% Change</td>
<td>Post</td>
<td>39.8</td>
<td>43.5</td>
<td>41.5</td>
<td>43.4</td>
<td>41.2</td>
</tr>
</tbody>
</table>

### All Site Groundlayer Means

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre or Post % Change</th>
<th>Understory Removal</th>
<th>Light Thinning</th>
<th>Group Shelterwood</th>
<th>Moderate Thinning</th>
<th>Woodland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groundlayer Cover (%)</td>
<td>Pre</td>
<td>43.4 ± 6.6</td>
<td>57.0 ± 6.3</td>
<td>60.0 ± 6.1</td>
<td>58.8 ± 5.6</td>
<td>45.0 ± 4.5</td>
</tr>
<tr>
<td></td>
<td>Post</td>
<td>81.4 ± 5.4</td>
<td>96.6 ± 3.6</td>
<td>86.0 ± 4.3</td>
<td>94.2 ± 3.8</td>
<td>96.2 ± 6.1</td>
</tr>
<tr>
<td>% Change</td>
<td>Post</td>
<td>+ 87.6%</td>
<td>+ 69.6%</td>
<td>+ 68.6%</td>
<td>+ 60.2%</td>
<td>+ 113.7%</td>
</tr>
</tbody>
</table>

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Table 2

Mean values and standard errors of seedling survival, growth, and leaf traits by treatment for the Ryerson study site. P-values of ANOVA analysis performed on the transformed data are provided.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Survival (%)</th>
<th>Height Growth (cm)</th>
<th>Diameter Growth (mm)</th>
<th>Basal Area Growth (cm²)</th>
<th>Seedling Leaf Count</th>
<th>Leaf Area (cm²)</th>
<th>Total Leaf Area (cm²)</th>
<th>Dry Leaf Mass (g)</th>
<th>SLA (cm²/g)</th>
<th>LMA (mg/m²)</th>
<th>Carbon Content (%)</th>
<th>Nitrogen Content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Understory Removal</td>
<td>43.2 ± 5.5</td>
<td>21.9 ± 3.4</td>
<td>4.3 ± 0.4</td>
<td>0.007 ± 0.0007</td>
<td>17.2 ± 3.1</td>
<td>18.2 ± 0.9</td>
<td>551.3 ± 60.6</td>
<td>0.31 ± 0.02</td>
<td>82.5 ± 2.1</td>
<td>0.016 ± 0.0019</td>
<td>44.4 ± 0.4</td>
<td>2.14 ± 0.06</td>
</tr>
<tr>
<td>Light Thinning</td>
<td>52.8 ± 4.1</td>
<td>22.1 ± 2.4</td>
<td>4.6 ± 0.4</td>
<td>0.008 ± 0.0008</td>
<td>24.2 ± 3.8</td>
<td>18.1 ± 1.8</td>
<td>575.3 ± 82.2</td>
<td>0.34 ± 0.04</td>
<td>57.2 ± 2.2</td>
<td>0.018 ± 0.0006</td>
<td>47.9 ± 0.2</td>
<td>2.26 ± 0.04</td>
</tr>
<tr>
<td>Group Shelterwood</td>
<td>45.1 ± 5.4</td>
<td>29.2 ± 2.7</td>
<td>5.0 ± 0.5</td>
<td>0.008 ± 0.0009</td>
<td>27.0 ± 2.6</td>
<td>17.5 ± 0.9</td>
<td>611.3 ± 40.4</td>
<td>0.35 ± 0.02</td>
<td>54.2 ± 2.6</td>
<td>0.018 ± 0.0007</td>
<td>47.9 ± 0.4</td>
<td>2.07 ± 0.09</td>
</tr>
<tr>
<td>Moderate Thinning</td>
<td>45.1 ± 5.4</td>
<td>26.1 ± 3.2</td>
<td>4.0 ± 0.3</td>
<td>0.007 ± 0.0006</td>
<td>24.1 ± 3.6</td>
<td>16.6 ± 0.9</td>
<td>551.9 ± 74.3</td>
<td>0.30 ± 0.1</td>
<td>61.5 ± 2.3</td>
<td>0.017 ± 0.0006</td>
<td>47.8 ± 0.2</td>
<td>2.18 ± 0.12</td>
</tr>
<tr>
<td>Woodland</td>
<td>50.1 ± 3.8</td>
<td>25.7 ± 2.5</td>
<td>4.1 ± 0.3</td>
<td>0.007 ± 0.0006</td>
<td>27.2 ± 3.1</td>
<td>19.6 ± 1.5</td>
<td>600.8 ± 111.2</td>
<td>0.39 ± 0.02</td>
<td>51.9 ± 1.5</td>
<td>0.020 ± 0.0005</td>
<td>47.5 ± 0.1</td>
<td>1.88 ± 0.06</td>
</tr>
<tr>
<td>P-value</td>
<td>0.768</td>
<td>0.300</td>
<td>0.551</td>
<td>0.437</td>
<td>0.142</td>
<td>0.862</td>
<td>0.871</td>
<td>0.086</td>
<td>0.014 *</td>
<td>0.019 *</td>
<td>0.036</td>
<td>0.07 *</td>
</tr>
</tbody>
</table>

Table 2

Mean values and standard errors of seedling survival, growth, and leaf traits by treatment for the Ryerson study site. P-values of ANOVA analysis performed on the transformed data are provided.
Figure 2
Treatment means ± SE for environmental conditions in the understory and canopy at all three study sites: (A) Total canopy basal area presented as meters squared per hectare, (B) Proportion change in canopy basal area, (C) Proportion of transmitted PAR (The below canopy transmitted photosynthetically active radiation divided by the above canopy Photosynthetically active radiation). Greyscale gradient relates to treatment intensity (based on canopy basal area removal). Letters above bars indicate significant differences among treatment means based on a pairwise comparison test.
Figure 3

Treatment means ± SE for environmental conditions in the understory and canopy at the Ryerson study site: (A) Volumetric Water Content, (B) Soil Temperature, (C) Maximum Atmospheric Temperature. Color gradients relate to the amount of basal area removed from the treatments. Greyscale gradient relates to treatment intensity (based on canopy basal area removal). Letters above bars indicate significant differences among treatment means based on a pairwise comparison test.
Figure 4

Treatment means ± SE for planted seedling survival and growth in the understory and canopy at all three study sites: (A) Seedling Survival, (B) Height Growth between pre-treatment and post-treatment measurements, (C) Diameter base growth between pre-treatment and post-treatment measurements, (D) Seedling Basal Area Growth between pre-treatment and post-treatment measurements. Height growth did not meet the assumptions for an ANOVA, and so a non-parametric Kruskall-Wallace test was performed. Greyscale gradient relates to treatment intensity (based on canopy basal area removal).
Figure 5

Treatment means ± SE for environmental conditions in the understory and canopy at Ryerson study site: (A) Mean Leaf Area, (B) Leaf Mass Area, (C) Specific Leaf Area, (D) Nitrogen Content of seedling leaves, (E) Carbon content of seedling leaves. Greyscale gradient relates to treatment intensity (based on canopy basal area removal). Letters above bars indicate significant differences among treatment means based on pairwise comparison test.
Figure 6

Treatment means ± SE for relative stem density of oak seedlings 5 years post thinning. Greyscale gradient relates to treatment intensity (based on canopy basal area removal).
Table 3

Ranking of linear mixed effects models relating survival and growth of planted seedlings to environmental conditions; only models with $\Delta$AIC < 2 are presented. Predictors are listed in decreasing order of predictive strength. AIC weight demonstrates the probability that the given models the best model (Burnham and Anderson, 2002). Marginal $R^2$ values are those associated with fixed effects. The conditional $R^2$ are those of the fixed effects plus the random effects (Site: TU).

<table>
<thead>
<tr>
<th>Survival Variables</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Marginal $R^2$</th>
<th>Conditional $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLI + percentcover</td>
<td>927.93</td>
<td>0</td>
<td>0.37</td>
<td>0.07</td>
<td>0.55</td>
</tr>
<tr>
<td>GLI + changeBA + percentcover</td>
<td>928.27</td>
<td>0.33</td>
<td>0.31</td>
<td>0.08</td>
<td>0.56</td>
</tr>
<tr>
<td>GLI + canopyBA + changeBA + percentcover</td>
<td>929.38</td>
<td>1.45</td>
<td>0.18</td>
<td>0.09</td>
<td>0.55</td>
</tr>
<tr>
<td>GLI + canopyBA + percentcover</td>
<td>929.91</td>
<td>1.98</td>
<td>0.14</td>
<td>0.07</td>
<td>0.55</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Height Growth Variables</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Marginal $R^2$</th>
<th>Conditional $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLI + changeBA + percentcover</td>
<td>821.0125</td>
<td>0</td>
<td>0.47</td>
<td>0.14</td>
<td>0.43</td>
</tr>
<tr>
<td>GLI + percentcover</td>
<td>822.5462</td>
<td>1.53</td>
<td>0.22</td>
<td>0.11</td>
<td>0.41</td>
</tr>
<tr>
<td>GLI + canopyBA + changeBA + percentcover</td>
<td>822.8636</td>
<td>1.85</td>
<td>0.19</td>
<td>0.14</td>
<td>0.42</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Diameter at Base Growth Variables</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Marginal $R^2$</th>
<th>Conditional $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLI + percentcover</td>
<td>111.8473</td>
<td>0</td>
<td>0.29</td>
<td>0.04</td>
<td>0.24</td>
</tr>
<tr>
<td>GLI + canopyBA + percentcover</td>
<td>112.5932</td>
<td>0.75</td>
<td>0.20</td>
<td>0.05</td>
<td>0.27</td>
</tr>
<tr>
<td>GLI + changeBA + percentcover</td>
<td>113.3043</td>
<td>1.46</td>
<td>0.14</td>
<td>0.05</td>
<td>0.26</td>
</tr>
</tbody>
</table>

GLI – Gap Light Index  
canopyBA – Total canopy basal area by plot  
percentcover – Percent cover of groundlayer species averaged by plot  
changeBA – Change in basal area between pre- and post-treatment
**Table 4**

Ranking of linear mixed effects models relating survival and growth of planted seedlings to leaf traits at the Ryerson site; only models with $\Delta$AIC <2 are presented. Predictors are listed in decreasing order of predictive strength.

<table>
<thead>
<tr>
<th>Survival</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Conditional $R^2$</th>
<th>Marginal $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLI + canopyBA + percentcover</td>
<td>922.21</td>
<td>0.00</td>
<td>0.44</td>
<td>0.55</td>
<td>0.09</td>
</tr>
<tr>
<td>GLI + canopyBA + changeBA + percentcover</td>
<td>922.44</td>
<td>0.23</td>
<td>0.40</td>
<td>0.54</td>
<td>0.14</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Height Growth</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Conditional $R^2$</th>
<th>Marginal $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLI + canopyBA + percentcover</td>
<td>844.58</td>
<td>0.00</td>
<td>0.37</td>
<td>0.38</td>
<td>0.11</td>
</tr>
<tr>
<td>GLI + canopyBA + changeBA + percentcover</td>
<td>844.74</td>
<td>0.16</td>
<td>0.34</td>
<td>0.40</td>
<td>0.16</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Diameter at Base Growth</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Weight</th>
<th>Conditional $R^2$</th>
<th>Marginal $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>par + percentcover</td>
<td>437.95</td>
<td>0.00</td>
<td>0.82</td>
<td>0.21</td>
<td>0.01</td>
</tr>
<tr>
<td>par + canopyBA + percentcover</td>
<td>441.06</td>
<td>3.10</td>
<td>0.17</td>
<td>0.21</td>
<td>0.01</td>
</tr>
</tbody>
</table>

- drymass – Averaged mass of dried planted seedling leaves
- lma – Averaged leaf mass area
- la - Averaged leaf area by plot (cm$^3$)
- N –Nitrogen content of leaves averaged by plot (%)
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**Appendix I**

Illustration of the random block design. This design was chosen to minimize the effect of variability within treatment conditions and potential confounding, resulting in better estimates of treatment effects. This experiment contained 120 plots in 40 treatment units for 5 treatments repeated at three sites in Lake County, IL.

A)  

B)  

**Appendix II**

Correlation matrix of all data collected for A) Ryerson Site only and B) All site data.
Appendix III

Ranking of linear mixed effects models relating survival and growth of planted seedlings to environmental conditions at the Ryerson site; only models with ΔAIC < 2 are presented. Predictors are listed in decreasing order of predictive strength.
Appendix IV

Data on natural regeneration of oak seedlings at all three of the study sites. Mean relative stem density shows the mean ± SE for the relative stem density by treatment (total oak seedling stems < 1 cm dbh / total woody stems < 1 cm dbh). Absolute stem density shows the total number of tree seedlings (absolute stem density) as stem/ha within each treatment and the direction and percent of change between pre-treatment and post-treatment monitoring.

### Natural Oak Regeneration

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre or Post</th>
<th>Understory Removal</th>
<th>Light Thinning</th>
<th>Group Shelterwood</th>
<th>Moderate Thinning</th>
<th>Woodland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Relative Stem Density</td>
<td>Pre</td>
<td>0.26 ± 0.08</td>
<td>0.16 ± 0.06</td>
<td>0.16 ± 0.06</td>
<td>0.18 ± 0.06</td>
<td>0.17 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>Post</td>
<td>0.16 ± 0.06</td>
<td>0.18 ± 0.06</td>
<td>0.12 ± 0.05</td>
<td>0.24 ± 0.08</td>
<td>0.23 ± 0.07</td>
</tr>
<tr>
<td>Absolute Stem Density (stems/ha)</td>
<td>Pre</td>
<td>106.25</td>
<td>267.20</td>
<td>110.45</td>
<td>370.87</td>
<td>123.46</td>
</tr>
<tr>
<td></td>
<td>Post</td>
<td>55.42</td>
<td>119.60</td>
<td>53.18</td>
<td>103.48</td>
<td>118.08</td>
</tr>
<tr>
<td>% Change</td>
<td></td>
<td>- 48 %</td>
<td>- 55 %</td>
<td>- 52 %</td>
<td>- 72 %</td>
<td>- 4 %</td>
</tr>
</tbody>
</table>