



Dynamics and determinants of *Quercus alba* seedling success following savanna encroachment and restoration

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ABSTRACT

The scattered tree layer that defines savannas is important for structuring the understory community and determining patterns of overstory recruitment. However, encroachment by woody plants has altered overstory tree densities and regeneration dynamics. We characterized seedling success of the savanna-forming species *Quercus alba* within Midwestern (USA) oak savannas that had been degraded by encroachment (control; $n = 4$) or experimentally restored by removal of encroaching woody vegetation (treatment; $n = 4$). In early 2004, 981 seedlings were transplanted along transects radiating from tree boles of overstory *Q. alba* trees to inter-canopy gaps and monitored for three growing seasons. Seedlings in restored sites had greater survival ($>2\times$), height growth (by $>50\%$), and basal diameter growth (by $>20\%$). In general, seedling survival and growth parameters increased with distance from overstory trees and were greatest in inter-canopy gaps of restored sites. By the final growing season (2006), the seedling survival-by-distance from tree correlation was stronger in control ($r^2 = 0.25$) than treatment sites ($r^2 = 0.18$), due to relatively uniform (and greater) survival at all distances from trees in treatment sites. In 2006, growth parameters (seedling height, diameter, Δ height, Δ diameter, and # leaves) were significantly (and more strongly) positively correlated with distance from trees in treatment sites. However, seedling herbivory was also greater after treatment and increased with distance from overstory trees. To understand seedling/microenvironment relationships, we created logistic (survival) and linear regression models (Δ height, Δ basal diameter, # leaves in 2006). Control seedling models had consistently greater predictive power and included more variables, suggesting that savanna restoration may decouple seedlings from their microenvironments, potentially by decreasing competition for limiting resources. Encroachment of the savannas in this study is limiting regeneration of *Q. alba*, suggesting substantially altered regeneration dynamics from those under which these savannas originally formed. Initial responses from our test of restoration, however, were promising and mechanical encroachment removal may be a means to promote overstory regeneration of this species. Finally, the savannas in this study appear inherently unstable and a scattered canopy tree configuration is unlikely to persist without regular disturbance, even in the restoration sites. Repeated mechanical thinning treatments with selected retention of recruiting *Q. alba* individuals or reintroduction of understory fire or grazing animals may be potential mechanisms for promoting long-term persistence of savannas at these sites.

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1. Introduction

Savannas occupy nearly one-third of the terrestrial globe, including >50 Mha in temperate regions of North America (McPherson, 1997; Scholes and Archer, 1997). Although represented by many different species, scattered or clustered overstory trees in low densities are a defining feature of all savannas (Scholes

and Archer, 1997). Savanna trees are important for structuring understory plant communities through their modification of understory microclimate (including understory light and soil moisture levels), soil nutrients, and species composition (Scholes and Archer, 1997; Breshears, 2006). Through direct influences on microclimate and indirect effects on competing understory plants, savanna overstory trees also impact patterns of tree regeneration; however, impacts vary among savanna ecosystems. Due to variation in water availability, savanna trees may facilitate seedling survival below canopies in more xeric savanna ecosystems (e.g., Borchert et al., 1989; Hoffmann, 1996; Weltzin and McPherson, 1999) or limit recruitment to inter-canopy gaps by out-competing seedlings, as is often true in more mesic savannas

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(e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Holmgren et al., 2000). The effects of canopy trees on recruitment may result in savanna overstory densities that range from relatively stable (e.g., Weltzin and McPherson, 1999) to largely unstable, with a tendency toward canopy gap infilling (e.g., Archer, 1990).

One striking consequence of instability has been woody (e.g., brush) encroachment. Over the last century many savanna ecosystems have been encroached by woody species due to a combination of fire suppression, altered grazing regimes, and climate change (Archer et al., 1988; Abrams, 1992; Scholes and Archer, 1997; Bustamante et al., 2006). Encroachment has increased overstory tree density and canopy cover and has altered tree composition, since encroaching species are frequently different than the pre-encroachment overstory dominants (Archer, 1990; Abrams, 1992). Encroachment may disrupt understory resource and vegetation patterns (Breshears, 2006). Presumably, patterns of recruitment may also differ after encroachment; however, recruitment patterns in encroached savannas are not well understood. Furthermore, although removal of encroaching vegetation can restore at least some understory resource and vegetation dynamics (Brudvig and Asbjornsen, in press), it is not well known how encroachment removal impacts patterns of savanna tree recruitment. Understanding recruitment implications of encroachment and removal will be critical for restoring remnants.

Midwestern oak savannas historically occupied 10–13 Mha as an ecotone between North American prairie grasslands to the west and deciduous forests to the east (Nuzzo, 1986). A scattered oak overstory and a continuous herbaceous understory are maintained by frequent understory fires; however, Midwestern oak savannas have largely been either converted to agriculture or degraded by woody encroachment resulting from fire suppression during the past 150 years (Nuzzo, 1986). Less than 1% remains intact and non-encroached, making Midwestern oak savannas a priority for conservation and restoration (Nuzzo, 1986). Due to fluctuations in climate and ensuing expansion and contraction of North American prairies, the precise range of Midwestern oak savannas has varied in size and position during that last 10,000 years (Clark et al., 2001). Thus, Midwestern oak savannas are interesting for studying recruitment dynamics, as they naturally exhibit range expansion (favorable recruitment periods) and contraction (non-favorable recruitment periods).

In this paper, we investigate spatial seedling dynamics within a large-scale Midwestern (USA) *Quercus alba* (white oak) savanna restoration experiment. We transplanted *Q. alba* seedlings into oak savannas with a prominent *Q. alba* overstory component that had been degraded by woody encroachment and into oak savannas that had been restored by mechanically removing woody encroachment. We then monitored seedlings for three growing seasons to address the following research questions: (1) what are the effects of restoration on seedling success (defined by survival and growth parameters)? (2) Does success vary along gradients from overstory *Q. alba* tree boles to inter-canopy gaps and is this influenced by restoration? (3) How does microenvironment at the level of the individual seedling influence seedling success and how are these relationships influenced by restoration? By answering these questions, we elucidate impacts of encroachment and restoration on savanna overstory recruitment patterns and stability.

2. Materials and methods

2.1. Site description

We conducted this study within a large-scale oak savanna restoration experiment, initiated in 2002 (Brudvig and Asbjornsen,

2007). Sites ($n = 8$) ranged in size from 1.5 to 3.3 ha and were located along the western shore of Saylorville Lake, a flood control reservoir near Des Moines, IA, USA (41°76'N, 93°82'W). These sites historically supported oak savannas with low densities of *Q. macrocarpa* (bur oak) and *Q. alba* overstory trees (Asbjornsen et al., 2005) and although never plowed, were grazed by cattle for ~100 years until purchase by the U.S. Army Corps of Engineers between 1965 and 1975 (Karnitz and Asbjornsen, 2006). Following purchase, sites were unmanaged and subsequently encroached by fire sensitive, shade tolerant tree species over the next several decades (e.g., *Ostrya virginiana*, *Fraxinus americana*, *Ulmus americana*; Karnitz and Asbjornsen, 2006), which filled inter-canopy gaps and resulted in overstory canopy closure (Brudvig and Asbjornsen, 2007). Soils were a mosaic of the Hayden (Glossic Hapludalf; developed under oak/hickory forest) and Lester series (Mollic Hapludalf; developed under oak savanna; United States Department of Agriculture, 2008). Des Moines' annual averages are 10 °C, 882 mm of precipitation, and 133 frost-free days (National Oceanic and Atmospheric Administration, 2008).

To remove woody encroachment, two sites received the restoration treatment during winter 2002–2003, whereby all non-*Quercus* woody vegetation >1.5 m tall and ranging in diameter from <1 to >50 cm was cut with chain saws and burned in off-site slash piles. Cut stumps were not treated with herbicides. Two additional sites received the restoration treatment in winter 2003–2004 and the remaining four sites were kept as unmanipulated controls. Two years were necessary to conduct the restoration treatment because it took approximately two months to treat each site and treatments were only conducted during winter, when the soil was frozen and disturbance was minimized.

Past work at these sites has quantified changes to the overstory and understory communities and structure. Encroachment removal reduced canopy cover from 84–89% to 8–52%, basal area from 14–37 m²/ha to 2–27 m²/ha, and significantly altered overstory composition in favor of *Quercus* species (Brudvig and Asbjornsen, 2007). In control sites, canopy cover (84–92%) and basal area (16–27 m²/ha) were unchanged during this time period (Brudvig and Asbjornsen, 2007). Following removal, canopy cover values fell within the published range for Midwestern oak savannas (Packard, 1993). By three years after treatment, understory cover had increased to over 80% and species richness had increased to 14–21 species/m² in treatment sites, compared to understory cover <20% and richness of 8–11 species/m² in control sites (Brudvig, in press; Brudvig and Asbjornsen, 2007).

2.2. Data collection

In early April 2004, we randomly selected 10 open-grown *Q. alba* overstory trees (canopy radius >6 m) from level uplands at each of the eight sites. For each tree, we established two randomly oriented transects, starting at the tree bole and extending 1.5× the distance to the canopy edge (see Brudvig and Asbjornsen, 2005 for details on canopy measurements). Along each transect, we transplanted one *Q. alba* seedling every 2 m, starting 0.5 m from the tree bole. This resulted in 5–6 seedlings/transect. For each tree, we also transplanted three seedlings at 3× the distance to the canopy edge, oriented in an equilateral triangle with sides 2 m long (hereafter 'gap seedlings'), in the same direction as one of the sampling transects. This resulted in a total of 981 transplanted seedlings (hereafter, 'full data set'). Seedlings were 2-0 bare root-stock and of central Iowa genotype, obtained from the Iowa Department of Natural Resources state forest nursery (Ames, IA). For each seedling, we collected the following data in July 2004–2006: basal diameter at the root collar, height (ground to tip of the highest live stem), number of leaves (2005 and 2006 only) and

herbivory (2005 and 2006 only; recorded as the percentage of leaf area missing due to herbivory, estimated in quartiles).

We collected microenvironment data for a subsampled set of transplanted seedlings (hereafter, 'microenvironment seedlings data set'). We subsampled by randomly selecting one seedling transect and one 'gap seedling' for five of the trees at each site. We established a permanently marked 1 m × 1 m understory plot around each of these 241 seedlings which was sampled during July 2004–2006 for species richness and cover by understory vegetation (woody plants <50 cm tall and all herbaceous vegetation regardless of height), leaves, bare ground, and down woody material.

During 2006, we also sampled overstory canopy cover and soils at each of these plots. To quantify canopy cover, we collected hemispherical photographs at 1.5 m above each plot during cloudless early morning hours in July. We used a Coolpix 900 camera and 270° fisheye lens, leveled and oriented with the plane of the film facing north. We analyzed photographs for canopy cover with HemiView Canopy Analysis Software Version 2.1 (Delta-T Devices Ltd.). To quantify soil properties, we collected a composite soil sample for each plot in July (eight subsamples/plot sample: one from each plot corner and one from the midpoint of each plot side). Samples were taken to 10 cm with a 1.9 cm diameter push probe and analyzed for texture, using a LaMotte field texture kit, to determine the percentages of sand (particle diameter ≥0.10 mm), silt (<0.10, ≥0.0002 mm), and clay (<0.0002 mm). Samples were then analyzed by Ward Lab (Kearney, NE) for pH, organic matter, nitrate N, total P, and K. We used a Theta Probe (Delta-T Devices Ltd.) to sample volumetric soil moisture content (e.g., soil water content; hereafter 'soil moisture') within each plot during four rain-free periods (26–28 April, 15–19 May, 2–6 June, 4–8 July), each following a rainfall >0.6 cm. The first sampling period was shortened from five to three days due to a second rain storm.

2.3. Data analysis

To test research questions 1 (effects of restoration on seedlings) and 2 (effects of distance from overstory trees-by-restoration on seedlings), we used split-plot analysis of variance (ANOVA) and split-plot repeated measures ANOVA (PROC GLM, SAS, 2002) with the 'all seedlings' data set. In the split-plot ANOVA, the independent variables were restoration treatment (main effect; site [treatment] as error term) and distance from the overstory tree (split-plot effect; tested with residual error), and the dependent variables were Δ seedling height and Δ seedling basal diameter. Δ seedling height and Δ seedling basal diameter were assessed for seedlings alive in 2006, relative to 2004 values, and calculated as: $([2006 \text{ measurement} - 2004 \text{ measurement}] / 2004 \text{ measurement}) \times 100$. In the split-plot repeated measures ANOVA, the independent variables were restoration treatment (main-plot effect; year × site [treatment] as error term), distance from overstory tree (split-plot effect; tested with residual error), and year (repeated effect), and the dependent variables were seedling survival (% originally planted) and means for seedling height, basal diameter, number of leaves, and herbivory for each year of study. In the case of significant treatment effects, we used *a priori* linear contrasts to test between treatment groups and treatment-by-distance from overstory tree. In addition, to test for directionality of seedling response along transects, we used linear regression (PROC REG, SAS, 2002) to compare treatments across distances from overstory tree for seedling survival, Δ seedling height, and Δ seedling basal diameter. For both ANOVA and regression analyses, independent variables were means/site-by-distance from overstory tree.

To test research question 3 (relationships between microenvironment, restoration, and seedling success), we created logistic and

linear regression models using the microenvironment seedlings data set. The 'all seedlings' and 'microenvironment seedlings' data sets did not differ for 2006 survival ($t = 1.43$, $p = 0.16$), Δ height ($t = 0.01$, $p = 0.99$), Δ basal diameter ($t = 0.08$, $p = 0.94$), or 2006 # leaves ($t = 1.59$, $p = 0.12$) suggesting that the subsample adequately reflected the entire data set. We evaluated models separately for seedlings in control and treatment sites, to address interactions between treatment and microenvironment. For seedling survival, we used backward logistic regression (PROC LOGISTIC, SAS, 2002). For Δ seedling height (log transformed), Δ seedling basal diameter (log transformed), and number of leaves in 2006, we used stepwise linear regression (PROC REG, SAS, 2002). In each regression, we fit the following plot-level variables: covers by understory vegetation, leaves, and bare ground in 2004, 2005, and 2006; minimum, maximum and average recorded soil moisture; % visible sky; soil pH, OM, N, P, K; % sand and silt; and total richness of understory species recorded in 2004, 2005, and 2006. We retained variables in the final models based on $p < 0.1$.

3. Results

3.1. Research questions 1 and 2: seedling success with restoration, distance from trees

Seedling survival was greater in treatment sites and this varied across years and distances from overstory trees (Table 1 and Fig. 1). After no evidence for a difference in seedling survival in 2004, survival was greater in treatment sites in 2005 (estimated effects size 21.6%) and 2006 (estimated effects size 38.1%), as rates of survival dropped to 27.3% in control sites, but only 67.8% in treatment sites by the end of the study. There was no evidence for interactions of treatment × distance from overstory tree or treatment × year × distance from overstory tree on seedling survival (Table 1). There was no correlation between survival and distance from overstory tree in 2004 or 2005 for treatment or control sites (maximum $r^2 = 0.08$, $p = 0.16$; treatment 2004). By 2006, however, rates of survival were positively correlated with distance from trees in control ($r^2 = 0.25$, $p = 0.0095$) and treatment sites ($r^2 = 0.18$, $p = 0.023$).

Averaged across years, seedling height was greater in treatment sites; however, there was an effect of year and treatment × year (Table 1). Height was greater in control sites in 2004 (estimated effects size: 1.2 cm; $t = 2.03$, $p = 0.049$), not different in 2005 (estimated effects size: 0.2 cm; $t = 0.13$, $p = 0.89$), and greater in treatment sites in 2006 (estimated effects size: 12.7 cm; $t = 8.95$, $p < 0.0001$). Distance from overstory tree influenced seedling height, whereas treatment × distance from overstory tree, year × distance from tree and treatment × year × distance from tree were not significant (Table 1). Δ Height was greater in treatment sites (Table 2; estimated effect size: 53.3%; $t = 7.53$, $p < 0.0001$), with significant differences in Δ height between treatments for all distances from overstory tree except directly next to tree boles (Fig. 2a). There was no evidence for an effect of distance from overstory tree or treatment × distance from tree on Δ height (Table 2). There was no correlation between height and distance from overstory tree in 2004 (treatment: $r^2 = 0.004$, $p = 0.75$; control: $r^2 = 0.08$, $p = 0.18$), or in 2005 for control sites ($r^2 = 0.09$, $p = 0.16$). Seedling height was positively correlated with distance from trees in treatment sites in 2005 ($r^2 = 0.22$, $p = 0.013$) and 2006 ($r^2 = 0.28$, $p = 0.0034$) and in control sites in 2006 ($r^2 = 0.18$, $p = 0.038$).

Averaged across years, seedling basal diameter was greater in treatment sites; however, there was an effect of year and treatment × year (Table 1). Basal diameter was greater in treatment sites in 2004 (estimated effects size: 0.40 mm; $t = 2.89$, $p = 0.0064$)

Table 1

Results of split-plot repeated measures ANOVA comparing *Quercus alba* performance in restored (treatment) and woody encroached (control) oak savannas, along transects from tree boles to inter-canopy gaps (canopy position), during three years of study.

Source of variation	d.f.	Survival	Height	Basal diameter	Leaves	Herbivory
		F/p	F/p	F/p	F/p	F/p
Treatment	1	86.02/<0.0001	34.78/<0.0001	5.76/0.022	151.19/<0.0001	6.18/0.018
Site (treatment)	6	9.46/<0.0001	2.95/0.021	2.11/0.08	3.40/0.01	3.65/0.0071
Canopy position	6	5.71/0.0003	3.50/0.009	1.58/0.19	5.38/0.0006	0.52/0.79
Treatment × canopy position	6	0.72/0.63	0.73/0.63	1.07/0.40	2.58/0.037	2.49/0.04
Among subjects error	32					
Year	2	276.97/<0.0001	16.12/<0.0001	23.53/<0.0001	13.25/0.001	0.67/0.42
Year × treatment	2	40.73/<0.0001	62.37/<0.0001	8.26/0.0006	62.00/<0.0001	1.88/0.18
Year × site (treatment)	12	4.56/<0.0001	2.50/0.0092	1.41/0.19	4.07/0.0038	4.08/0.0038
Year × canopy position	12	4.47/<0.0001	1.33/0.22	2.09/0.030	2.57/0.038	1.25/0.31
Year × treatment × canopy position	12	1.54/0.13	0.87/0.58	2.11/0.029	2.57/0.038	1.46/0.22
With subjects error	64					

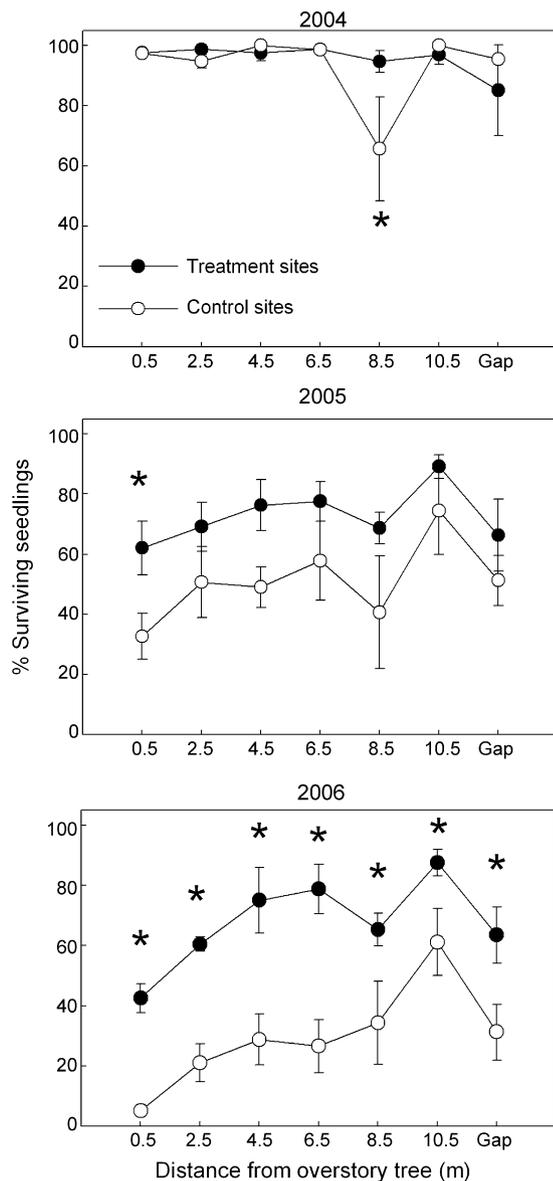


Fig. 1. Oak seedling survival (% of original planted; total $n = 981$) by year in restoration (treatment) and woody encroached (control) oak savannas, along transects from tree boles to inter-canopy gaps (distance from overstory tree). Values are means per site ($n = 4$ /treatment, control) \pm 1 S.E. Significant canopy position differences between treatments denoted by * (independent linear contrast; $p < 0.05$).

and 2006 (estimated effects size: 1.41 mm; $t = 5.50$, $p < 0.0001$), but there was no evidence for a difference in 2005 (estimated effects size: 0.51 mm; $t = 0.87$, $p = 0.39$). There was no evidence for effects of distance from overstory tree or treatment \times distance from tree on seedling basal diameter. Year \times distance from overstory tree and treatment \times year \times distance from tree were significant (Table 1), as basal diameter increased with distance from trees, especially in treatment sites (Fig. 2a). Across years, Δ basal diameter was greater in treatment sites (Table 2; estimated effect size: 22.1%; $t = 3.48$, $p = 0.0013$), with significant differences between treatment and control sites at further distances from overstory trees and in gap plots (Fig. 2b). There was an impact of distance from overstory tree, but not treatment \times distance from tree on Δ basal diameter (Table 2). There was no evidence for a correlation between basal diameter and distance from trees in 2004 or 2005 for treatment or control sites (maximum $r^2 = 0.07$, $p = 0.17$; treatment 2005). By 2006, however, basal diameter increased with distance from trees in treatment sites ($r^2 = 0.45$, $p = 0.0001$), with a trend for a positive correlation in control sites ($r^2 = 0.14$, $p = 0.07$).

Treatment, distance from overstory tree, and their interaction influenced seedling leaf number (Table 1). Seedlings in treatment sites supported more leaves than in control sites and in 2006 the magnitude of these differences was more pronounced with increasing distance from trees (Fig. 3). There were significant effects of year and year \times treatment on leaf number (Table 1), as seedlings in treatment sites had more leaves and the magnitude of this difference increased with time (2005 estimated effects size: 1.86 leaves, $t = 5.58$, $p < 0.0001$; 2006 estimated effects size: 7.00 leaves; $t = 9.19$, $p < 0.0001$; Fig. 3). Furthermore, we found evidence for year \times distance from overstory tree and year \times treatment \times distance from tree interactions (Table 1), as leaf number was greater at further distances from trees in 2006, with greater magnitudes of difference in treatment sites (Fig. 3). Leaf number was positively correlated with distance from trees in treatment sites, with stronger evidence in 2006 (2005: $r^2 = 0.09$, $p = 0.11$; 2006: $r^2 = 0.35$, $p = 0.0009$). We found the

Table 2

Results of split-plot ANOVA comparing changes in *Quercus alba* seedling height and basal diameter in restored (treatment) and woody encroached (control) oak savannas, along transects from tree boles to inter-canopy gaps (canopy position).

Source of variation	d.f.	Δ Height	Δ Basal diameter
		F/p	F/p
Treatment	1	68.52/<0.0001	17.58/0.0002
Site (treatment)	6	1.92/0.11	2.26/0.063
Canopy position	6	2.08/0.083	3.23/0.013
Treatment \times canopy position	6	0.85/0.55	1.79/0.13
Error	32		

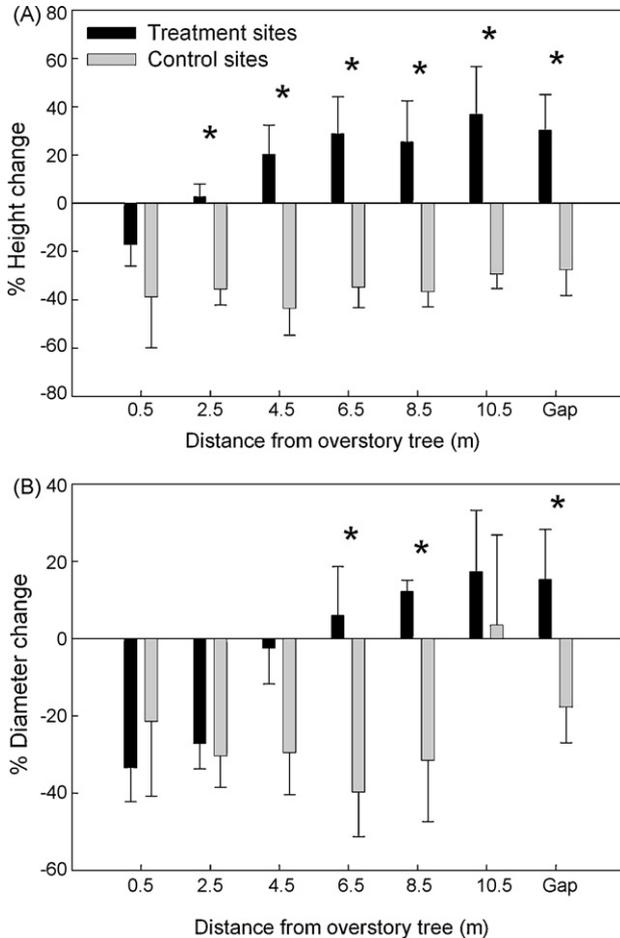


Fig. 2. Relative changes in *Quercus alba* seedling height (A) and basal diameter (B) during three growing seasons in restored (treatment) and woody encroached (control) oak savannas, along transects from tree boles to inter-canopy gaps (distance from overstory tree). Values are means per site ($n=4$ /treatment, control) ± 1 S.E. Significant canopy position differences between treatments denoted by * (independent linear contrast; $p < 0.05$).

reverse in control sites, as there was evidence for a correlation in 2005 ($r^2 = 0.13$, $p = 0.086$), but none in 2006 ($r^2 = 0.04$, $p = 0.33$).

Treatment influenced rates of seedling herbivory, as seedlings had lower levels of herbivory in control sites in 2006 (Table 1; estimated effects size: 0.30; $t = 2.28$, $p = 0.029$). Although there was no effect of distance from overstory tree, the treatment \times distance from tree interaction was significant (Table 1). There was no evidence that year, year \times distance from tree, or year \times treatment \times distance from tree had significant effects on herbivory. Herbivory levels were positively correlated with distance from trees in treatment sites (2005: $r^2 = 0.39$, $p = 0.0004$; 2006: $r^2 = 0.35$, $p = 0.0009$), while we found no strong support for a correlation in control sites (2005: $r^2 = 0.08$, $p = 0.17$; 2006: $r^2 = 0.04$, $p = 0.35$).

3.2. Research question 3: seedling/microenvironment relationships

The final logistic regression models significantly predicted seedling survival, producing 71.8% concordance with observed values in treatment sites and 83.4% in control sites (Table 3). In treatment sites, survival was positively correlated with 2006 vegetation cover and mean soil moisture and negatively correlated with 2005 vegetation cover (Table 3). In control sites, survival was positively correlated with 2006 vegetation and leaf cover and understory species richness in all years (2004, 2005, 2006) and negatively correlated with % silt (Table 3).

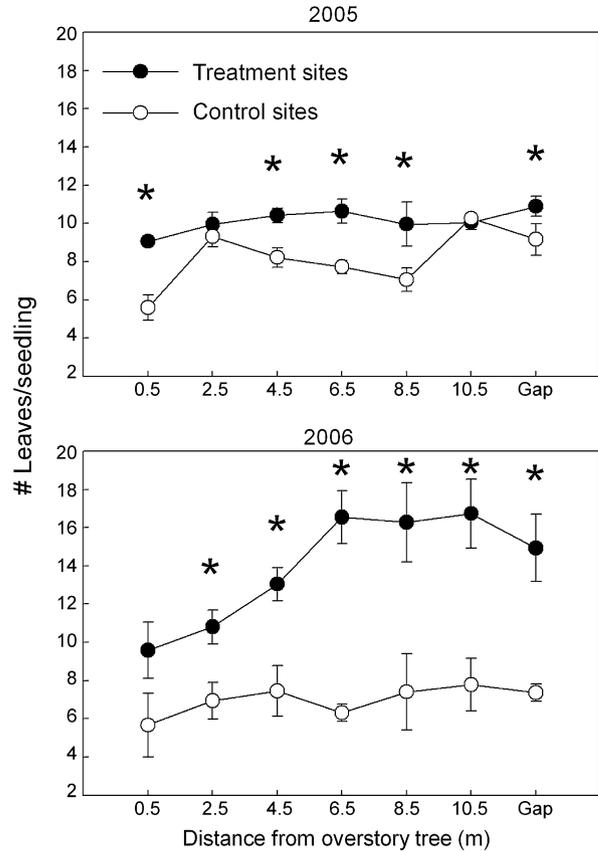


Fig. 3. Number of leaves per *Quercus alba* seedling in restored (treatment) and woody encroached (control) oak savannas, along transects from tree boles to inter-canopy gaps (distance from overstory tree). Values are means per site ($n=4$ /treatment, control) ± 1 S.E. Significant canopy position differences between treatments denoted by * (independent linear contrast; $p < 0.05$).

Linear regression models significantly predicted seedling Δ height, Δ basal diameter, and 2006 # leaves in treatment and control sites (Table 4). More than 40% of the variance was explained by all three models in control sites, but predictive power was modest for 2006 # leaves in treatment sites ($r^2 = 0.19$), and weak for Δ height and Δ basal diameter at treatment sites ($r^2 < 0.10$). In treatment sites: Δ height was positively associated with 2006 understory species richness; Δ basal diameter was positively associated with 2006 vegetation cover and negatively with pH; and 2006 # leaves was positively associated with 2006 vegetation cover and 2005 bare ground and negatively with minimum soil moisture (Table 4 and Fig. 4). In control sites: Δ height was positively associated with pH and 2006 bare ground and negatively associated with 2004 bare ground; Δ basal diameter was positively associated with mean soil moisture and pH and negatively with soil N and 2004 understory species richness; and 2006 # leaves was positively associated with 2005 understory species richness and negatively with 2004 richness (Table 4 and Fig. 4).

4. Discussion

4.1. Research question # 1: what are the effects of restoration on seedling success?

Oak savanna restoration had a pronounced positive effect on *Q. alba* seedling success. Compared to seedlings in encroached sites, seedlings in restored sites had $>2\times$ greater survival and increased more in height and basal diameter ($>50\%$ and $>20\%$, respectively).

Table 3

Results of backward logistic regression for *Quercus alba* seedling survival in treatment (restored) and control (woody encroached) oak savannas. Treatment model χ^2 (Wald) = 13.63, 3 d.f., $p = 0.0035$; 71.8% concordance with observed values. Control model χ^2 (Wald) = 22.59, 6 d.f., $p = 0.0009$; 83.4% concordance with observed values.

	Variable	Parameter estimate \pm S.E.	Wald χ^2/p	Live/dead ^a
Treatment	Intercept	-2.68 \pm 1.29	4.30/0.038	
	Vegetation 2005 (% cover)	-0.042 \pm 0.015	8.02/0.0046	61.4/60.9
	Vegetation 2006	0.051 \pm 0.016	10.47/0.0012	66.9/56.8
	Mean % soil moisture	0.14 \pm 0.06	5.35/0.021	22.1/20.5
Control	Intercept	-2.11 \pm 1.55	1.85/0.17	
	Vegetation 2006	0.061 \pm 0.025	5.90/0.015	17.4/10.0
	Leaves 2006	0.040 \pm 0.013	7.82/0.0052	66.0/58.4
	% Silt	-0.077 \pm 0.025	9.88/0.0017	34.3/42.8
	Richness 2004	0.30 \pm 0.13	5.34/0.021	8.9/9.0
	Richness 2005	0.17 \pm 0.10	2.90/0.089	10.3/9.2
	Richness 2006	0.34 \pm 0.15	5.04/0.025	6.5/5.1

^a Values are means for plots with surviving/non-surviving seedlings.

Table 4

Results of stepwise linear regression for *Quercus alba* Δ seedling height, Δ seedling basal diameter, and 2006 # leaves in treatment (restored) and control (woody encroached) oak savannas.

	d.f.	Model F/p	Model r^2	Factor	Parameter estimate \pm S.E.	Partial $r^2/F/p$
Δ Seedling height	1/84	8.08/0.0056	0.088	Intercept	3.56 \pm 0.31	$F = 135.79, p < 0.0001$
				Richness 2006	0.064 \pm 0.022	0.0877/8.08/0.0056
Control	3/23	5.27/0.0065	0.41	Intercept	-0.83 \pm 1.95	$F = 0.18, p = 0.67$
				pH	0.75 \pm 0.31	0.15/5.84/0.024
				Bare ground 2004	-0.02 \pm 0.0072	0.15/4.26/0.050
				Bare ground 2006	0.034 \pm 0.013	0.11/3.60/0.070
Δ Seedling diameter	2/83	3.99/0.0221	0.088	Intercept	5.90 \pm 1.045	$F = 31.91, p < 0.0001$
				Vegetation cover 2006	0.0079 \pm 0.0039	0.045/4.06/0.047
				pH	-0.35 \pm 0.16	0.043/3.79/0.055
				Control	4/22	4.31/0.0100
Mean soil moisture	0.13 \pm 0.05	0.12/3.75/0.065				
pH	0.73 \pm 0.35	0.11/4.41/0.047				
N	-0.18 \pm 0.051	0.11/2.96/0.098				
Richness 2004	-0.083 \pm 0.038	0.10/3.43/0.077				
2006 # leaves	3/82	6.57/0.0005	0.19	Intercept	13.73 \pm 7.46	$F = 3.39, p = 0.069$
				Minimum soil moisture	-0.90 \pm 0.39	0.11/9.86/0.0023
				Vegetation cover 2006	0.17 \pm 0.056	0.057/5.68/0.019
				Bare ground 2005	0.14 \pm 0.081	0.0313/3.18/0.0782
Control	2/24	7.88/0.0023	0.40	Intercept	6.27 \pm 2.05	$F = 9.40, p = 0.0053$
				Richness 2004	-0.76 \pm 0.27	0.21/8.22/0.0085
				Richness 2005	0.96 \pm 0.24	0.19/5.85/0.023

Furthermore, these patterns strengthened over time. By the final year of study, seedling mortality stabilized in treatment, but not control sites. Between 2005 and 2006 >95% of seedlings survived in treatment sites, whereas roughly half of control site seedlings died during this period. Differences in height, basal diameter and # leaves were most pronounced in the final year of study, suggesting that these discrepancies may continue to increase in future years.

These findings support woody encroachment removal as a potential means to promote *Q. alba* regeneration in savannas. This is dually important, given the paucity of knowledge about restoration of encroached savannas and the widespread decline in *Q. alba*, and *Quercus* sp. in general, over the last century in North America (Abrams, 1992, 2003). However, since savannas are defined by a broken overstory (Scholes and Archer, 1997), it will be critical that restoration promotes proper rates of overstory regeneration. Too rapid a rate of recruitment will result in encroachment, whereas too slow a rate may result in canopy tree loss. At this point, it is unclear how rates of *Q. alba* regeneration relate to rates of overstory mortality. This issue is highlighted by a recent review of California

savanna-forming *Quercus* species, where concerns over population declines were called into question (Tyler et al., 2006). These researchers noted that, given the long-lived nature of these species (multiple centuries; similar to *Q. alba*), only infrequent regeneration is needed to offset overstory mortality. Our study represents a first assessment of how savanna restoration influences recruitment patterns and more work is needed to understand impacts of restoration on canopy tree dynamics.

Savannas are characterized by co-occurring trees and herbaceous vegetation and numerous studies have attempted to understand their coexistence (Scholes and Archer, 1997). In our study, restoration promoted *Q. alba* seedling growth and survival, despite concomitant four-fold increases in understory vegetation cover (Brudvig and Asbjornsen, 2007), which included promotion of both woody and herbaceous species (Brudvig, in press). Thus, it appears that reduced overstory competition may have been more important to seedling success than increased understory competition. In general, reducing overstory density is suggested for promoting *Quercus* sp. regeneration (Johnson et al., 2002); however, relatively

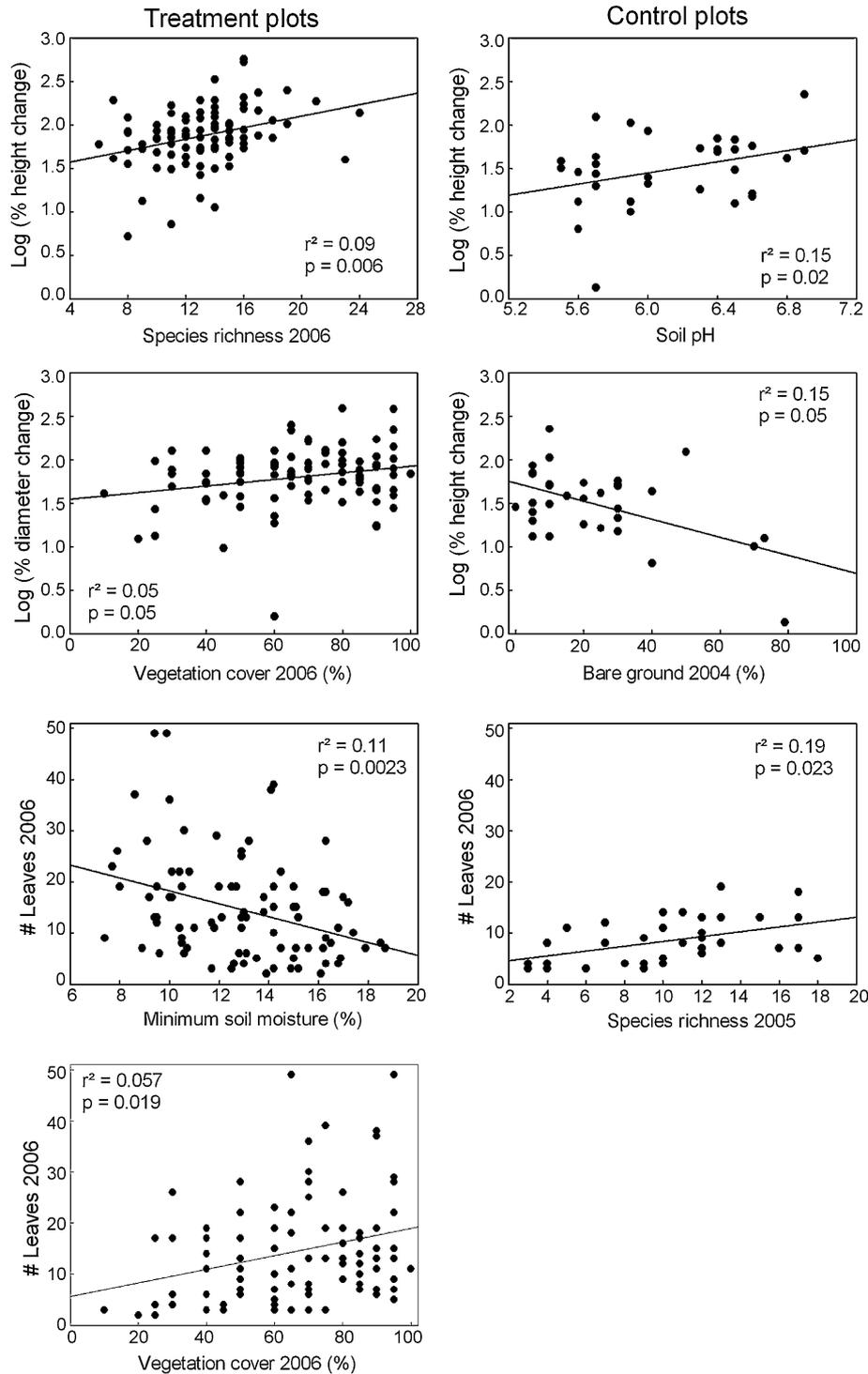


Fig. 4. Correlations between *Quercus alba* seedling parameters and plot factors from stepwise linear regression models for restored (treatment) and woody encroached (control) oak savanna sites. Species richness and vegetation cover values are for 1 m × 1 m plots surrounding transplanted *Q. alba* seedlings. Partial r^2 values are presented.

few studies have investigated both effects of overstory and understory competition on tree seedling success. Our results are generally consistent with Buckley et al. (1998), who found that overstory removal was more important than understory removal for promoting *Quercus rubra* seedlings in *Pinus* and *Quercus* stands. Conversely, Davis et al. (1999) determined that two *Quercus* sp. had greater survival in shaded plots and when competing herbaceous vegetation had been removed, suggesting that water availability was limiting in their experimental old-field system.

4.2. Research question # 2: does seedling success vary with distance from overstory *Q. alba* trees and is this influenced by restoration?

In general, *Q. alba* seedlings performed better at further distances from overstory trees, regardless of treatment; however, restoration interacted with distance from overstory tree to influence seedling success. By the final growing season, seedling survival (control sites), height (treatment and control sites), basal diameter (treatment sites), and # leaves (treatment sites)

increased with distance from the tree. Survival did not correlate with distance from trees in treatment sites due to more uniform (and greater) values across all distances from trees, though survival was somewhat reduced immediately adjacent to tree boles. Increased seedling performance with distance from overstory trees has been reported in other mesic savanna ecosystems and this is generally thought to be a function of reduced competition between seedlings and overstory vegetation (e.g., Borchert et al., 1989; Holmgren et al., 2000; Brudvig and Asbjornsen, 2005, 2008). In control sites, gap-phase recruitment dynamics (commonly associated with closed-canopy forests) may be more important, whereby recruitment is rare and limited to larger tree-fall gaps (e.g., Cho and Boerner, 1991). If this is the case, persistent seedling survival will be critical until canopy disturbances permit seedling release. This mechanism is not promising for recruitment at our encroached savanna sites, as seedling survival was reduced below 30% after only three growing seasons.

Savanna restoration interacted with distance from tree to increase seedling herbivory. Potentially, this was influenced by seedlings leaf defense, as soil nitrate N levels increased following restoration (Brudvig, 2007). N fertilization can reduce C-based leaf phenolic levels, which deter herbivores (Dudt and Shure, 1994). Past work with *Quercus* sp. has shown increased lepidopteron herbivory rates in seedlings below canopy trees, due to transfer of insects to seedlings (Humphrey and Swaine, 1997; Wada et al., 2000); however, our results are not consistent with these patterns. Our classification system for herbivory (% of leaf missing) is consistent with detection of arthropod herbivory in *Q. alba* (e.g., Marquis and Whelan, 1994); however, mammalian browse damage also contributed to seedling damage (Brudvig, personal observation) and the relative contributions of the two are unknown. Past studies have found both positive and negative correlations between insect herbivory and *Q. alba* seedling performance. Marquis and Whelan (1994) demonstrated reduced seedling biomass after insect defoliation, whereas Adams and Rieske (2001) found that arthropod feeding contributed more to herbivory levels than mammalian herbivory, but did not impact *Q. alba* seedling growth. Thus, although herbivory was influenced by restoration, it is unknown what effect this might have on regeneration.

Our study contributes to literature on savanna stability and overstory tree distributions. In general, savanna systems with strong nurse-tree effects (i.e., facilitation of seedlings below overstory trees) are thought to be more stable than savanna systems where recruitment occurs in inter-canopy gaps, as recruitment is constrained to areas previously occupied by overstory vegetation (Weltzin and McPherson, 1999). We found strong evidence that overstory recruitment will occur away from overstory trees. Thus, the restored oak savannas in this study do not appear stable. After investigation of the full regenerating community, Brudvig and Asbjornsen (2007) similarly argue that the oak savannas at these sites represent an alternative (encroached) stable state. However, reintroduction of prescribed fire may help to restore stable overstory dynamics (Higgins et al., 2000). In a closely related savanna system, Rebertus and Burns (1997) reported reduced oak seedling survival in inter-canopy gaps during prescribed surface fires, due to greater fuel loading. How fire might interact with the factors we studied is unknown; however, many Midwestern savannas are managed with fire, making this an important future research direction.

4.3. Research questions # 3: how does microenvironment influence seedling success and is this influenced by restoration?

Models of survival and growth parameters at control sites had consistently (and sometimes dramatically) greater explanatory

power than models for treatment sites. Furthermore, in most cases, control site models contained more significant variables than treatment seedling models. Potentially, resources were plentiful enough after restoration that seedling performance was somewhat decoupled from microenvironment. One such resource is light. Strong asymmetric competition for light exists in forested ecosystems (Weiner, 1990) and low understory light levels can reduce *Q. alba* recruitment (Johnson et al., 2002; Abrams, 2003). Interestingly, % visible sky was not a significant component of any of the models. Potentially, we captured major differences in understory light levels by dividing the data set into control and treatment seedlings, since % visible sky increased dramatically with restoration (Brudvig and Asbjornsen, in press). If this were the case, seedling response to understory light may be represented by the treatment-level differences. Indeed, a logistic regression model of survival of control and treatment site seedlings together (data not presented) showed seedlings survival to be positively correlated with visible sky, understory cover, and understory species richness, all of which increased with restoration (Brudvig and Asbjornsen, 2007; Brudvig, in press).

Understory vegetation cover was correlated with seedling performance, especially in treatment sites. Past work has found that understory vegetation can either inhibit (Davis et al., 1999; Germaine and McPherson, 1999) or facilitate (Tonioli et al., 2001) savanna seedlings; however, understory removal generally improves seedling performance in forested systems (e.g., Lorimer et al., 1994; Buckley et al., 1998). Given that we did not manipulate understory cover, this correlation may simply reflect that certain microsites were favorable for many understory plants, including *Q. alba* seedlings. Our results are consistent with Götmark (2007), who found *Q. robur* and *Q. petraea* survival during oak woodland restoration to be positively correlated with understory herb cover, a result attributed to covariance between understory oak and herb performance in favorable microsites.

We found a positive correlation between mean soil moisture and seedling survival in treatment sites and Δ basal diameter in control sites, which was somewhat surprising at our relatively mesic sites. Numerous other studies have linked soil moisture and savanna seedling success; however, most of these occurred either in semi-arid regions or on sandy substrates (e.g., Davis et al., 1999; Tonioli et al., 2001). We also found a negative correlation between minimum soil moisture and # leaves in treatment sites. Although counterintuitive, we suggest that this might be tied to canopy position. Although canopy interception reduced maximum soil moisture levels under trees in treatment areas, these plots also dried less quickly than areas further away from trees (Brudvig and Asbjornsen, in press). Thus, this pattern might result from seedlings in shadier plots (close to trees) displaying reduced leaf productivity, despite reduced soil moisture deficit during dry periods (Asbjornsen et al., 2004).

5. Conclusions

The results of this study suggest that woody encroachment limits regeneration by the overstory dominant savanna tree, *Q. alba*. This is especially concerning given widespread declines of *Q. alba* throughout central and eastern North America during the last century (Abrams, 2003). Fire suppression is generally implicated for low rates of oak regeneration in North America (Abrams, 1992) and this may be a factor in our Midwestern oak savanna sites. However, we found evidence that restoration by removal of encroaching woody vegetation may promote *Q. alba* regeneration in Midwestern oak savannas, suggesting that this might be an effective fire surrogate. Furthermore, we extend the importance of overstory thinning for oak regeneration from silviculture (Johnson

et al., 2002) to restoration. Johnson et al. (2002) summarize a vast body of oak ecology and silviculture literature and much of this might apply to oak savanna ecology and restoration. However, it is important to note that silviculture and restoration objectives can differ, as do the ecology of forests, the focus of most past oak research, and savanna systems. While promoting maximum recruitment is a primary concern during oak silviculture, savanna restoration must result in far lower overstory recruitment rates. Furthermore, the spatial configuration of overstory recruitment is of interest to savanna ecology. In our study, seedlings performed better at further distances from overstory trees, providing evidence for inherent instability. Our results are consistent with those of other mesic savanna systems (e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Holmgren et al., 2000), whereas past work in arid savannas has shown stronger nurse-tree effects (Scholes and Archer, 1997). This suggests two things. First, savanna restoration strategies should consider site fertility. This point is particularly germane to work with *Q. alba*, which occurs across a wide gradient of soil moisture conditions, from relatively xeric to mesic (Abrams, 1992). Second, it will be important to understand the full set of interacting disturbances in savanna systems, so that they might be restored. Fire and grazing by large-bodied herbivores were historically important forces that shaped Midwestern North America (Axelrod, 1985) and understorey fires are important for regeneration dynamics in Midwestern oak savannas (Peterson and Reich, 2001). Future research might investigate the role of thinning treatments, like the one in this study, as fire surrogates, perhaps in combination with prescribed burning or grazing treatments, to concomitantly control woody encroachment and promote oak regeneration.

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References

- Abrams, M.D., 1992. Fire and the development of oak forests. *BioScience* 42, 346–353.
- Abrams, M.D., 2003. Were has all the white oak gone? *BioScience* 53, 927–939.
- Adams, A.S., Rieske, L.K., 2001. Herbivory and fire influence white oak (*Quercus alba* L.) seedling vigor. *Forest Sci.* 47, 331–337.
- Archer, S., Scifres, C., Bassham, C.R., 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58, 111–127.
- Archer, S., 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. *J. Biogeography* 17, 453–462.
- Asbjornsen, H., Vogt, K.A., Ashton, M.S., 2004. Synergistic responses of oak, pine and shrub seedlings to edge environments and drought in a fragmented tropical highland oak forest, Oaxaca, Mexico. *Forest Ecol. Manag.* 192, 313–334.
- Asbjornsen, H., Brudvig, L.A., Mabry, C.M., Evans, C.W., Karnitz, H.M., 2005. Defining reference information for restoring ecologically rare tallgrass oak savannas in the Midwest. *J. Forest* 103, 345–350.
- Axelrod, D.I., 1985. Rise of the grassland biome, central North America. *Botanical Rev.* 51, 163–201.
- Borchert, M.I., Davis, F.W., Michaelsen, J., Dee Oyler, L., 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70, 389–404.
- Breshears, D.D., 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? *Front Ecol. Environ.* 4, 96–104.
- Brudvig, L.A. Woody encroachment removal from Midwestern oak savannas alters understorey diversity across space and time. *Restoration Ecol.*, doi:10.1111/j.1526-100X.2008.00431.x in press.
- Brudvig, L.A., 2007. Effects of restoration on Midwestern oak savanna biodiversity, structure, and oak regeneration. Ph.D. Dissertation, Iowa State University, Ames.
- Brudvig, L.A., Asbjornsen, H., 2005. Oak regeneration before and after initial restoration efforts in a tall grass oak savanna. *Am. Midland Nat.* 153, 180–186.
- Brudvig, L.A., Asbjornsen, H., 2007. Stand structure, composition and regeneration dynamics following removal of encroaching woody vegetation from Midwestern oak savannas. *Forest Ecol. Manag.* 244, 112–121.
- Brudvig, L.A., Asbjornsen, H. The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas. *J. Appl. Ecol.*, in press.
- Brudvig, L.A., Asbjornsen, H., 2008. Patterns of oak regeneration in a Midwestern savanna restoration experiment. *Forest Ecol. Manag.* 255, 3019–3025.
- Buckley, D.S., Sharik, T.L., Isebrands, J.G., 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. *Ecology* 79, 65–78.
- Bustamante, M.M.C., Medina, E., Asner, G.P., Nardoto, G.B., Garcia-Montiel, D.C., 2006. Nitrogen cycling in tropical and temperate savannas. *Biogeochemistry* 79, 209–237.
- Cho, D.S., Boerner, R.E.J., 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. *Vegetatio* 93, 9–18.
- Clark, J.S., Grimm, E.C., Lynch, J., Mueller, P.G., 2001. Effects of the holocene climate change on the C4 grassland/woodland boundary in the northern plains, USA. *Ecology* 82, 620–636.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T., Muermann, C., 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water–light–nitrogen gradient. *Plant Ecol.* 145, 341–350.
- Dudt, J.F., Shure, D.J., 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology* 75, 86–98.
- Germaine, H.L., McPherson, G.R., 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower treeline, Arizona, U.S.A. *Ecoscience* 6, 92–99.
- Götmark, F., 2007. Careful partial harvesting in conservation stands and retention of large oaks favour oak regeneration. *Biol. Conserv.* 140, 349–358.
- Higgins, S.L., Bond, W.J., Trollope, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol.* 88, 213–229.
- Hoffmann, W.A., 1996. The effects of fire and cover on seedling establishment in a neotropical savanna. *J. Ecol.* 84, 383–393.
- Holmgren, M., Segura, A.M., Fuentes, E.R., 2000. Limiting mechanisms in the regeneration of the Chilean matorral. *Plant Ecol.* 147, 49–57.
- Humphrey, J.W., Swaine, M.D., 1997. Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. II. Insect defoliation of trees and seedlings. *J. Appl. Ecol.* 34, 585–593.
- Johnson, P.S., Shifley, S.R., Rogers, R., 2002. *The Ecology and Silviculture of Oaks*. CABI Publishing, New York.
- Karnitz, H.M., Asbjornsen, H., 2006. Composition and age structure of a degraded tallgrass oak savanna in central Iowa, USA. *Nat. Areas J.* 26, 179–186.
- Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82, 227–237.
- Marquis, R.J., Whelan, C.J., 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75, 2007–2014.
- McPherson, G., 1997. *Ecology and Management of North American Savannas*. University of Arizona Press, Tucson.
- National Oceanic and Atmospheric Administration, 2008. Comparative Climate Data. URL: www.ncdc.noaa.gov. Accessed 11 August, 2008.
- Nuzzo, V.A., 1986. Extent and status of midwest oak savanna: presettlement and 1985. *Nat. Areas J.* 6, 6–36.
- Packard, S., 1993. Restoring oak ecosystems. *Restoration Manag.* 11, 5–17.
- Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecol. Appl.* 11, 914–927.
- Rebertus, A.J., Burns, B.R., 1997. The importance of gap processes in the development and maintenance of oak savannas and dry forests. *J. Ecol.* 85, 635–645.
- SAS Institute, 2002. Version 9.00. SAS Institute, Cary, North Carolina.
- Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544.
- Tonioli, M., Escarré, J., LePart, J., Speranza, M., 2001. Facilitation and competition affecting the regeneration of *Quercus pubescens* Willd. *Ecoscience* 8, 381–391.
- Tyler, C.M., Kuhn, B., Davis, F.W., 2006. Demography and recruitment limitations of three oak species in California. *Q. Rev. Biol.* 81, 127–152.
- United States Department of Agriculture, 2008. Official Soil Series Descriptions. URL: <http://soils.usda.gov/soils/technical/classification/osd/index.html>. Accessed 11 August, 2008.
- Wada, N., Murakami, M., Yoshida, K., 2000. Effects of herbivore-bearing adult trees of the oak *Quercus crispula* on the survival of their seedlings. *Ecol. Res.* 15, 219–227.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5, 360–364.
- Weltzin, J.F., McPherson, G.R., 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecol. Monogr.* 69, 513–534.