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Patterns of oak regeneration in a Midwestern savanna restoration experiment

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Abstract

Savannas' defining feature is a scattered tree layer. However, woody plants have encroached savannas throughout the world, altering tree densities and potentially modifying regeneration dynamics. We used a replicated large-scale restoration experiment with Midwestern oak savannas (USA) to understand spatial patterns of regeneration by the dominant overstory species, *Quercus alba*. *Q. alba* is not only of interest as a savanna-forming species, but also a species of concern due to widespread low rates of regeneration. In this experiment, four sites received a restoration treatment, whereby all encroaching mesophytic trees and large shrubs were mechanically removed, and four sites operated as encroached controls. Within each site, we monitored naturally occurring *Q. alba* seedlings in plots under overstory trees and in plots in inter-canopy gaps for 4 years, including 1 year before and 3 years after treatment. Seedlings were ~5× more abundant below overstory *Q. alba* trees, which we attribute to seed-rain. There was no effect of restoration on seedling densities. Year-to-year survival and survival of seedlings tracked over the course of the study were greater in sites undergoing restoration. Four-year survival rates were 31% in treatment sites and 10% in control sites. Across all sites, seedlings survived equally as well under canopy trees as in inter-canopy gaps. Mean seedling height, basal diameter, and number of leaves were greater in sites undergoing restoration, relative to control sites, and in inter-canopy gaps, relative to under canopy trees. Furthermore, there was an interaction between treatment and plot type, whereby mean seedling attributes were greatest in inter-canopy gaps of treatment sites. Seedlings tracked over the course of this study displayed greater survival, Δ (change in) height, Δ basal diameter, and Δ number of leaves in treatment sites, relative to control sites, and greater survival, Δ basal diameter, and Δ number of leaves in inter-canopy gaps, relative to under canopy trees. Individual seedling survival, Δ basal diameter, and Δ number of leaves were greatest in inter-canopy gaps of treatment sites. Our study suggests that woody encroachment is limiting regeneration of *Q. alba* in savannas; however, this may be ameliorated by removal of encroaching woody vegetation. Thus, the act of restoring these savannas may hold promise for promoting regeneration of *Q. alba*. Finally, the restored savannas in this study appear inherently unstable, as seedlings performed best in inter-canopy gaps. Further work with prescribed fire and/or grazing may elucidate stable tree–herbaceous understory coexistence in Midwestern oak savannas.

Keywords: Canopy thinning; Midwestern oak savanna; *Quercus alba*; White oak; Woody encroachment removal

1. Introduction

Savannas are found throughout tropical and temperate portions of the world and are characterized by scattered overstory trees and a continuous herbaceous understory (Scholes and Archer, 1997). Various factors are thought to maintain open canopy structure and lead to tree–grass coexistence, including frequent droughts, elevational gradients, animal browsing, and understory fires (Scholes and Archer, 1997; Anderson, 1998; Weltzin and McPherson, 1999; Sankaran et al., 2004). Due to changes in these basic drivers, many savanna ecosystems have been altered by woody (brush) encroachment over the past century (Archer et al., 1988; Abrams, 1992; Scholes and Archer, 1997; Bustamante et al., 2006). This has led to canopy-gap infilling and subsequent modifications to understory vegetation and patterns of resource availability (Breshears, 2006). Although restoration efforts abound, there have been few empirical evaluations of methodologies.

North American oak (*Quercus*) savannas are of widespread conservation interest and, thus, represent excellent systems for

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testing restoration (Anderson, 1998). Prior to Euro-American settlement, oak savannas formed the ecotone between prairie grasslands and Eastern deciduous forests (Nuzzo, 1986; Anderson, 1998). Defined by a sparse, fire-maintained oak overstory and a continuous herbaceous understory, <1% of Midwestern oak savannas remain intact and non-encroached, due to agricultural conversion and fire suppression (Nuzzo, 1986). However, an unknown amount of Midwestern oak savannas has been encroached by mesophytic trees and shrubs, due to fire suppression and altered grazing regimes (Nuzzo, 1986; Anderson, 1998). Although this can result in canopy closure, these remnants may hold great promise for restoration, as the pre-encroachment oak trees generally remain intact and understory plants may respond rapidly to restoration (Asbjornsen et al., 2005). Restoration of encroached remnants generally involves mechanical removal of encroaching trees and shrubs, followed by reimplementation of an understory fire regime (Packard, 1993).

Oak savannas are further intriguing as experimental systems due to widespread concerns about regeneration of the genus *Quercus* (Loftis and McGee, 1993). Recruitment of oaks into the overstory has been minimal in many North American *Quercus* ecosystems, despite prevalent overstory components and abundant small seedlings in the understory (Abrams, 1992, 2003). Thus, in spite of abundant propagule supplies, improper conditions for recruitment threaten oak prominence in North America (Loftis and McGee, 1993). Relative to North American oak forests, far less is known about oak regeneration dynamics in Midwestern oak savannas. There is some evidence to suggest that the same general patterns might apply, as past studies have described savannas with overstory oak trees and abundant oak seedlings, but an absence of sapling-sized oak regeneration (e.g., Abrams, 1992; Russell and Fowler, 1999; Brudvig and Asbjornsen, 2005). However, more work is warranted to understand how important determinants of oak recruitment in forests, such as gap dynamics and overstory removal (e.g., Cho and Boerner, 1991; Ashton and Larson, 1996; Buckley et al., 1998) might apply to restoration of Midwestern oak savannas.

Since successful overstory replacement is a central goal of restoration efforts in savannas and other forested systems (SER, 2004; Asbjornsen et al., 2005), a benchmark for restoration success is overstory recruitment by the ecosystem's dominant tree species. Regeneration dynamics are central to savanna ecology and understanding patterns of overstory recruitment in savannas is important for determining their stability and likelihood for persistence. For example, Weltzin and McPherson (1999) demonstrated overstory stability and likely long-term persistence in Arizona, USA oak savannas, as overstory trees facilitated seedling emergence and growth by reducing evaporative losses, whereas seedling success in inter-canopy gaps was poor (see also Borchert et al., 1989; Hoffmann, 1996 for additional examples). Conversely, numerous studies have demonstrated instability in savannas, marked by recruitment in inter-canopy gaps and subsequent trends toward canopy infilling (e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Holmgren et al., 2000). Thus, savanna recruitment has important spatial components. However, implications of woody encroachment and encroachment removal for spatial patterns of savanna tree recruitment are not well understood. A better understanding of how patterns of regeneration by the dominant overstory tree species differ between encroached and restored savannas will be useful for evaluating restoration success.

In this study, we use a large-scale savanna restoration experiment to determine spatial patterns of survival and performance for *Quercus alba* (white oak) seedlings. Restoration began in 2002–03 with mechanical removal of woody encroachment from four of eight *Q. alba* savannas in Iowa, USA. Here, we expand upon a previous study (Brudvig and Asbjornsen, 2005) by doubling the number of sites and expanding the study from 2 to 4 years. Thus, although the analyses in the present study encompass some of the data presented in Brudvig and Asbjornsen (2005), we now provide a better replicated and ecologically more meaningful (1 versus 3 year response) assessment of restoration. Specifically, we investigate how restoration interacts with seedling location (under overstory trees versus in inter-canopy gaps) to impact seedling densities, mean seedling size, individual seedling survival, and performance of individual seedlings monitored over the course of the study.

2. Methods

2.1. Study area

This study was conducted along the western shore of Saylorville Lake, in central Iowa, USA (41°76′N, 93°82′W). In 2002, we established study sites in eight degraded oak savanna remnants, identified by large open-grown *Q. alba* overstory trees. Sites were located within ~8 km of each other, ranged in size from 1.5 to 3.3 ha, and were located on parallel upland ridges and separated by ravines supporting early successional and floodplain vegetation. Sites were never plowed and supported ~100 years of cattle grazing, which terminated after they were purchased 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 mesophytic tree species over the next several decades (e.g., *Ostrya virginiana*, *Fraxinus americana*, *Ulmus Americana*; Karnitz and Asbjornsen, 2006). 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, 2007). The nearby city of Des Moines supports annual averages of 10 °C, 882 mm of precipitation, and 133 frost-free days (National Oceanic and Atmospheric Administration, 2007).

2.2. Restoration methodology

We conducted the restoration treatment in four of eight study sites, with the remaining four sites functioning as (encroached) controls. The eight sites were situated in three general clusters, one of which contained four sites, and we randomly assigned half of the sites in each cluster to treatment and half to control status. Restoration involved the removal of all non-*Quercus* sp. woody stems >1.5 m tall, except at one site where *Quercus* and *Carya* species were retained. Encroaching woody vegetation was cut with chainsaws and burned in off-site slash piles by hand crews during winter months, when the soil was frozen. Due to this time constraint, two sites received the restoration treatment in 2002–03 and two during 2003–04. Brudvig and Asbjornsen (2007) describe woody species composition and stand structure before and for three subsequent years after encroachment removal. Briefly, basal area was reduced by 8.5–18.7 m^2/ha and canopy cover by 35.0–77.4%. Control sites' basal area (pre- and post-treatment: 17–27 m^2/ha) and canopy cover values (pre-treatment: 84–89%; post-treatment: 85–94%) remained relatively static during this time period. In treatment sites, basal area was reduced from 14–37 m^2/ha to 2–27 m^2/ha with treatment, whereas canopy cover was reduced from 84–87% to 8–52%. Following treatment, canopy cover values in treatment sites coincided with published definitions for Midwestern oak savannas (10–50%: Curtis, 1959; 10–30%: Packard, 1993). There was no herbicide applied following treatment and stump resprouting did occur for some species, most notably *Cornus racemosa* and *Ostrya virginiana* (response of the full woody species community are described in Brudvig and Asbjornsen, 2007).

2.3. Sampling methodology

We established 10 permanently marked ''canopy'' and 10 ''canopy-gap'' plots within each of the eight study sites. Canopy plots were located under randomly selected large, open-grown *Q. alba* overstory trees. For each tree, we measured the distance from the tree bole to the vertically projected canopy edge, in each of the four cardinal directions. We used the mean of these distances as a radius to create a circular sampling plot below each tree, with the tree bole as its center. Plot radii generally ranged from 4 to 6 m. Each canopy plot was paired with an equally sized canopy-gap plot. Canopy-gap plots were also circular, with plot centers three canopy radii from its associated tree. The direction to the canopy-gap plot was random, but constrained to areas not occupied by other *Quercus* canopy trees. By selecting plots in this manner, canopy-gap plots at treatment sites were located in areas lacking overstory canopy cover, after treatments were applied (i.e., in true canopy-gaps). In control sites, canopy-gap plots fell below a non-*Quercus* overstory (i.e., below canopies of encroaching trees).

We surveyed all plots for naturally occurring *Q. alba* seedlings in the year before and for three subsequent years after restoration. Since the restoration treatment was conducted in two different years, this resulted in two study periods. For the two treatment sites restored during winter of 2002–2003 and their two closest control sites, the study period was 2002–2005. For the remaining four sites, the study period was 2003–2006. Surveys were conducted each September, to assess seedlings at the end of the growing season. In the initial survey, we tagged and recorded height (vertical distance to the highest living point), basal diameter (at the root collar) and number of leaves for all *Q. alba* seedlings <50.0 cm tall. In subsequent surveys, we monitored all original seedlings (regardless of height) and tagged and monitored any new recruits for height, basal diameter, and number of leaves.

2.4. Data analysis

We tested for effects of restoration and canopy/canopy-gap plot types on *Quercus alba* seedlings using split-plot analysis of variance (ANOVA) and split-plot repeated measures ANOVA in SAS (2002). To test for changes in mean seedling values over the course of the study, we used split-plot repeated measures ANOVA, with restoration treatment (main-plot effect; site[-treatment] as error term), plot type (split-plot effect; tested with residual error), and year in the restoration sequence (repeated effect) as independent variables. Split-plot repeated measures ANOVA dependent variables were plot means for year-to-year seedling survival (% of seedlings surviving from one year to the next), seedling density, height, basal diameter, and number of leaves. In the case of significant treatment effects, we used independent linear contrasts to test between treatment groups and treatment × plot types. To understand how individual seedlings responded during the study, we used split-plot ANOVA, with restoration treatment (main effect) and plot type (split-plot effect) as independent variables. Split-plot ANOVA dependent variables were plot-level % survival, Δ (change in) seedling height, Δ seedling basal diameter, and Δ seedling leaves. Percent survival was defined as the percentage of seedlings surveyed in the first year of study that survived through the final year of study. For seedlings surviving through the duration of the study, we calculated Δ seedling height, Δ seedling basal diameter, and Δ seedling leaves as: ([final year measurement − first year measurement]/first year measurement) × 100. Prior to analyses, we log (value +1) transformed overall, new, and surviving seedling density values to normalize residuals. We averaged values for each plot type by site, to arrive at $n = 4$ replicates per treatment.

3. Results

3.1. Seedling densities

Across years, we observed 4.9× greater densities of *Q. alba* seedlings below *Q. alba* overstory trees (test of plot type: $F_{1,135} = 7.01$, $p = 0.0091$) and this pattern was consistent during all years of study (maximum $p = 0.03$; Fig. 1a). There was no evidence for an effect of treatment ($F_{1,6} = 0.67$, $p = 0.41$) or treatment × plot type on seedling densities ($F_{1,135} = 0.26$, $p = 0.61$). There was an effect of year*plot type on seedling densities ($F_{3,405} = 2.72$, $p = 0.044$). As this pattern was evident for new ($F_{2,270} = 2.92$, $p = 0.056$), but not surviving seedling densities ($F_{2,270} = 1.39$, $p = 0.25$; Fig. 2), we attribute this to a *Q. alba* mast year during 2004 (Brudvig, personal observation).

Overall densities of new and surviving seedlings were greater below *Q. alba* canopy trees ($F_{1,135} = 18.47$,

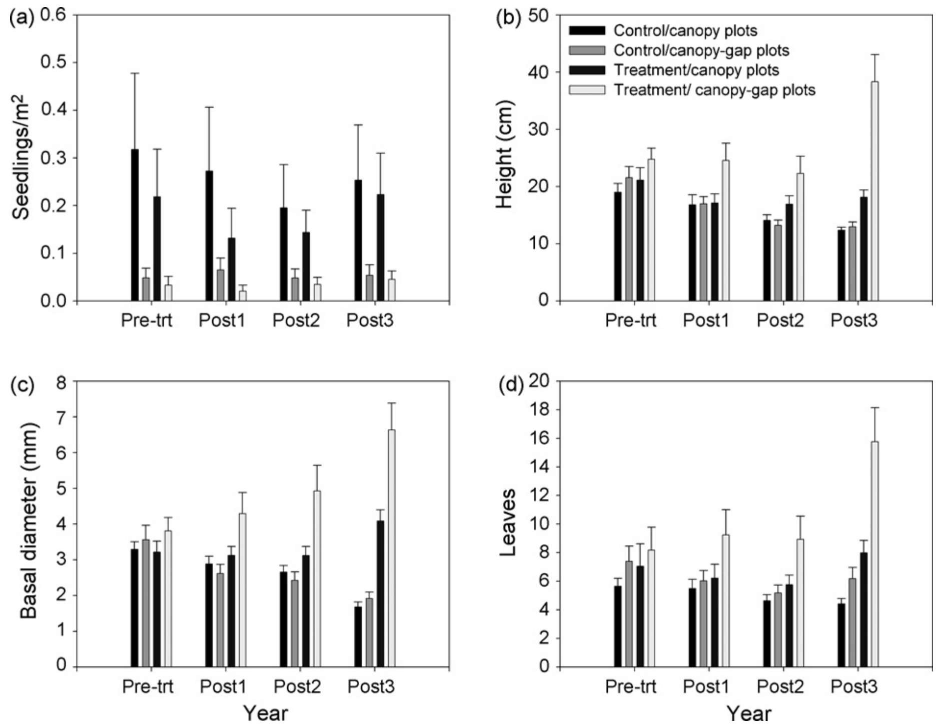

Fig. 1. Mean density (a), height (b), diameter (c), and number of leaves (d) for naturally occurring *Quercus alba* seedlings surveyed in plots under *Quercus alba* canopy trees (canopy plots; $n = 40$/treatment) or in plots away from trees (canopy-gap plots; $n = 40$/treatment) within an oak savanna restoration experiment. Values are site means ± 1 S.E.

$p < 0.0001$) and there was evidence for this pattern with surviving seedlings ($F_{1,135} = 3.57$, $p = 0.061$). There was evidence for this pattern during all years of study (maximum $p = 0.058$; Fig. 2). There was no evidence for an effect of treatment on the densities of new ($F_{1,6} = 0.09$, $p = 0.77$) or surviving seedlings ($F_{1,6} = 0.39$, $p = 0.53$), nor was there evidence for an effect of treatment × plot type on the densities of new ($F_{1,135} = 0.19$, $p = 0.67$) or surviving seedlings ($F_{1,135} = 0.72$, $p = 0.40$).

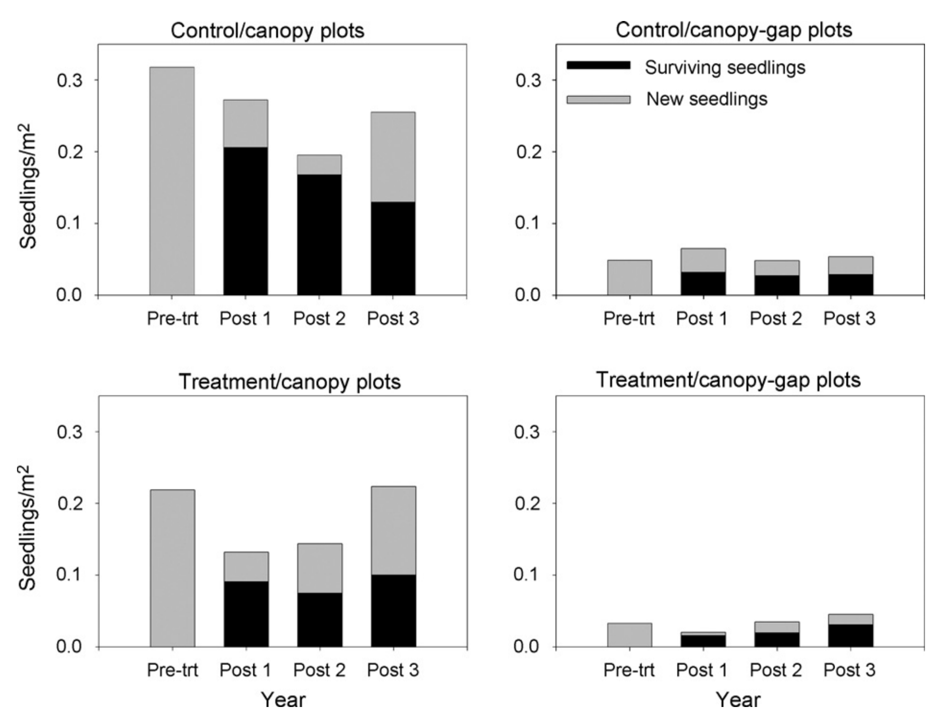

Fig. 2. Comparison of year-to-year seedling survival for plots under *Quercus alba* canopy trees (canopy plots; $n = 40$/treatment) or in plots away from trees (canopy-gap plots; $n = 40$/treatment) within an oak savanna restoration experiment.

3.2. Mean seedling values

Across years, mean seedling height ($F_{1,33} = 22.44$, $p < 0.0001$), basal diameter ($F_{1,33} = 19.20$, $p = 0.0001$), and number of leaves ($F_{1,33} = 8.37$, $p = 0.0067$) were greatest in canopy-gaps of treatment sites relative to all other plot types (Fig. 1). This result led to greater mean seedling height ($F_{1,6} = 23.55$, $p < 0.0001$), basal diameter ($F_{1,6} = 34.59$, $p < 0.0001$), and number of leaves ($F_{1,6} = 11.47$, $p = 0.0018$) in treatment sites, relative to control sites, and greater mean seedling height ($F_{1,33} = 26.72$, $p < 0.0001$), basal diameter ($F_{1,33} = 17.79$, $p = 0.0002$), and number of leaves ($F_{1,33} = 16.15$, $p = 0.0003$) in canopy-gaps, relative to under canopy trees (Fig. 1). These differences increased over time for mean seedling height (test of year $\times$treatment: $F_{3,15} = 24.84$, $p < 0.0001$; year $\times$ plot type: $F_{3,99} = 6.33$, $p = 0.0006$; year $\times$ treatment $\times$ plot type: $F_{3,99} = 8.64$, $p < 0.0001$), mean seedling basal diameter (year $\times$ treatment: $F_{3,15} = 34.14$, $p < 0.0001$; year $\times$ plot type: $F_{3,99} = 2.59$, $p = 0.057$; year $\times$ treatment $\times$ plot type: $F_{3,99} = 4.56$, $p = 0.0049$), and mean number of leaves (year $\times$ treatment: $F_{3,15} = 14.57$, $p < 0.0001$; year $\times$ plot type: $F_{3,99} = 4.83$, $p = 0.0035$; year $\times$ treatment $\times$ plot type: $F_{3,99} = 4.90$, $p = 0.0032$).

3.3. Seedling survival

Year-to-year seedling survival was influenced by restoration (test of treatment: $F_{1,6} = 16.90$, $p = 0.0002$), as treatment sites displayed greater seedling survival two years (estimated effects size: 37.2%; $t = 4.79$, $p < 0.0001$) and 3 years (estimated effects size: 25.2%; $t = 2.71$, $p = 0.01$) after treatment (Fig. 2). Due to non-significant differences in survival 1 year after treatment, there was an effect of year $\times$ treatment on seedling survival ($F_{2,10} = 5.06$, $p = 0.0089$); however, there was no evidence for an effect of year $\times$ plot type ($F_{2,70} = 0.75$, $p = 0.48$) or year $\times$ treatment $\times$ plot type ($F_{2,70} = 2.03$, $p = 0.14$).

A greater percentage of seedlings survived from the beginning until the end of the experiment in treatment (31.0%) than control sites (9.6%; $t = 2.25$, $p = 0.028$). There was no evidence for an effect of plot type ($F_{1,56} = 0.01$, $p = 0.93$) or treatment $\times$ plot type ($F_{1,56} = 0.10$, $p = 0.75$) and survival was similar in treatment site/canopy-gap plots (32.4%) and treatment site/canopy plots (29.5%). Control site/canopy plots (10.4%) and canopy-gap plots (8.8%) displayed lower 4-year survival.

3.4. Individual seedling growth parameters

Seedlings that survived from the beginning to the end of this study displayed greater height growth in treatment sites ($F_{1,5} = 21.38$, $p < 0.0001$), but we found no evidence for an effect of plot type ($F_{1,27} = 1.51$, $p = 0.23$) or treatment $\times$ plot type ($F_{1,27} = 1.30$, $p = 0.26$). Seedlings in treatment sites increased in height by an average of 102% more than seedlings in control sites (Fig. 3). Surviving seedlings had greater basal diameter growth in treatment relative to control sites ($F_{1,5} = 36.53$, $p < 0.0001$), in canopy-gaps relative to under canopy trees ($F_{1,27} = 4.75$, $p = 0.038$), and in treatment site/canopy-gaps relative to other plot types ($F_{1,27} = 4.81$, $p = 0.037$). Seedlings increased in basal diameter by an average of 80% more in treatment than control sites, 30% more in canopy-gaps than under canopy trees, and 59% more in treatment sites/canopy-gaps than any other plot type (Fig. 3). Surviving seedlings increased their number of leaves more in treatment relative to control sites ($F_{1,5} = 24.04$, $p < 0.0001$), and there was some evidence for seedlings growing more leaves in canopy-gaps relative to under canopy trees ($F_{1,27} = 3.22$, $p = 0.084$), and in treatment site/canopy-gaps relative to other plot types ($F_{1,27} = 2.64$, $p = 0.12$). Seedlings increased leaf numbers by an average of 126% more in treatment sites than in control sites, 47% more in canopy-gaps than under canopy trees, and 90% more in treatment sites/canopy-gaps than any other plot type (Fig. 3).

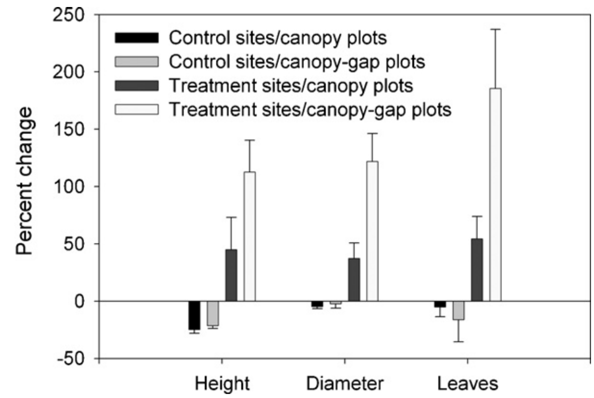

Fig. 3. Relative changes in *Quercus alba* seedling height, basal diameter, and number of leaves, for individual seedlings monitored for 4 years in plots under *Quercus alba* canopy trees (canopy plots; $n = 40$/treatment) or in plots away from trees (canopy-gap plots; $n = 40$/treatment) within an oak savanna restoration experiment. Values are site means $\pm$ 1 S.E.

4. Discussion

Removal experiments, like this one, represent opportunities for understanding the impacts that invading and encroaching species have on plant populations and communities (Díaz et al., 2003). In our case, directly measuring the encroachment process would have required ~30 years of study (Karnitz and Asbjornsen, 2006). We found reduced mean *Quercus alba* seedling performance (height, basal diameter, # leaves, collectively), reduced seedling survival, and no evidence for seedling height or basal diameter growth in savannas that had been encroached by mesophytic trees. Thus, our results suggest that savanna encroachment has had a profound negative impact on regeneration of the pre-encroachment dominant overstory tree species, *Q. alba*. Certainly, this is a major concern and suggests that, if current conditions persist, *Q. alba* may eventually be replaced entirely in this system by mesophytic tree species. However, this experiment also investigated seedling dynamics after restoration, involving removal of woody encroachment from savannas. Restoration increased mean seedling performance, increased rates of seedling survival, and promoted growth of *Q. alba* seedlings. Furthermore, we found that many of these differences between seedlings in treatment and control sites increased with time and were pronounced by the end of the study. Thus, our results provide evidence that *Q. alba* may successfully regenerate in restored sites.

This study also investigated the spatial consequences of woody encroachment and removal for *Q. alba* seedling dynamics. Although spatial elements of savanna tree recruitment have been frequently recognized and have important consequences for savanna stability (e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Weltzin and McPherson, 1999), our study is unique in providing an experimental test of canopy removal on seedling patterns. Like in other mesic savanna systems (e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Holmgren et al., 2000), *Q. alba* seedlings in our restored sites performed better in inter-canopy gaps. This has implications for patterns of regeneration and suggests that the savannas in this study may be inherently unstable, with a tendency toward canopy infilling even by savanna tree species like *Q. alba*. This is not a surprising result, as open canopy structure in Midwestern savannas is thought to be maintained by recurrent disturbances, such as understory fires, grazing pressures, and drought. In fact, the unstable nature of Midwestern savannas, in the absence of disturbance, is the very cause of their encroachment by mesophytic species (Anderson, 1998). Thus, our findings demonstrate that removal of woody encroachment might successfully restore characteristic patterns of overstory recruitment in these savannas. However, our findings also show that these recruitment patterns are severely disrupted by woody encroachment; we found no evidence for *Q. alba* seedling growth either under or away from overstory *Q. alba* trees in encroached sites. We suggest that encroachment removal is an important step in promoting a sustained oak overstory component; however, questions remain about maintaining the characteristically broken overstory at these sites through management over the long-term (Asbjornsen et al., 2005). Certainly, oaks must recruit at a sufficient rate to replace overstory mortality, but what that rate is and what types of management will allow for its achievement are presently unknown. This issue is highlighted by a recent review of California savanna-forming *Quercus* species, where the 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 (Tyler et al., 2006). Furthermore, we need to determine the consequences of management actions, like prescribed fire and grazing, for spatial patterns of oak recruitment and what these patterns will mean for long-term savanna dynamics. These questions warrant future research.

Although oaks are an important overstory component of temperate regions in North America, many of these systems have had chronically low levels of oak regeneration during the past half century (Abrams, 1992). This has spawned a variety of research and management directions to promote oak regeneration (e.g., Loftis and McGee, 1993). This is especially important for managing *Q. alba*, which is among the most ecologically and commercially important oak species (Abrams, 2003). We provide support for woody encroachment removal as a management tool for promoting oak regeneration. Our results suggest that past studies detailing the importance of gap-phase recruitment (e.g., Cho and Boerner, 1991; Ashton and Larson, 1996) and positive effects of silvicultural tree removal for *Quercus* species (e.g., Buckley et al., 1998) might pertain to management and restoration of oak savanna ecosystems. However, it should be noted that seedlings in our study performed well in spite of four-fold increases in understory vegetation density following the restoration treatment (Brudvig and Asbjornsen, 2007). As understory vegetation has been shown to be an important deterrent of oak regeneration in forests (Lorimer et al., 1994), this suggests that findings from closed canopy *Quercus* systems should be applied cautiously to savannas.

Similarly to many oak ecosystems, we found abundant levels of oak seedlings in the understory of the savannas in this study, especially under canopy *Q. alba* trees (Abrams, 1992). This pattern is likely due to propagule pressure from productive overstory trees. We suggest that our results have implications for land managers seeking to promote oak regeneration in encroached savannas. Surveys to determine densities and spatial patterns of naturally occurring oak seedlings should be performed prior to management decisions. If densities are sufficient in areas away from overstory oak trees, removal of encroaching trees may promote oak regeneration in inter-canopy gaps. However, if oak seedlings are confined to below overstory oak canopies, our results demonstrate that growth of these seedlings might be minimal, even after canopy opening. In this situation, we suggest that transplanting oak seedlings to inter-canopy gaps might be a fruitful means of promoting oak regeneration after encroachment removal.

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