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Stand structure, composition, and regeneration dynamics following removal of encroaching woody vegetation from Midwestern oak savannas

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Abstract

Woody encroachment has altered oak savannas throughout much of the Midwestern United States. To help understand restoration options, we assessed the impacts of mechanically removing encroaching mesophytic trees and shrubs on structure, composition, and regeneration dynamics in *Quercus alba* dominated oak savannas in Iowa ($n = 4$), relative to control sites ($n = 4$). We monitored stand structure and species composition for the seedling, shrub, sapling, and overstory tree strata for 1 year prior to and 3 years following mechanical removal of encroaching woody vegetation. There was no evidence for differences between treatment and control sites for any study variable prior to treatment implementation. The removal treatment resulted in increased cover by understory vegetation and concomitant reductions in cover by leaf litter and bare ground. Treatment altered overstory tree species composition (assessed by multi-response permutation procedure [MRPP]) in favor of oak species in all 3 years following removal, while shrub and sapling compositions were not statistically different from control sites until the third year following the removal treatment. Seedling composition was unaffected by treatments. We observed a recruitment pulse, with treated sites displaying increased density of shrubs 2 years after and saplings 3 years after removal of encroaching vegetation. Advanced regeneration (saplings size class) was dominated by two species: *Ostrya virginiana* and *Cornus racemosa*, which we attribute to vigorous vegetative reestablishment by stump resprouting. Seedlings of *Q. alba* increased in density throughout the course of this study; however, *Q. alba* shrub and sapling size classes were unaffected by treatment. We suggest that the encroached savannas in this study represent an alternative stable state, whereby regeneration is dominated by encroaching species even shortly after removal treatments. Continued research during future stages of restoration, which will include prescribed fire, may help to identify effective management options for controlling encroaching woody vegetation and promoting oak regeneration.

Keywords: Alternative stable states; Mechanical thinning; *Quercus alba*; Regeneration; Restoration; Woody encroachment

1. Introduction

Woody plant invasion and expansion are occurring in grasslands, savannas, and woodlands throughout North America (Archer et al., 1988; Archer, 1989; Abrams, 1992; Bowles and McBride, 1998; Nielsen et al., 2003), due to a combination of fire suppression, altered grazing regimes, and climate change (Abrams, 1992; Scholes and Archer, 1997). In oak (*Quercus*) ecosystems this has modified stand structure and species composition (Abrams, 1992). For example, in eastern North America, fire suppression and selective logging have led to the expansion of native mesophytic tree species into historically oak dominated woodlands, resulting in altered overstory species composition, introduction of a dense mid-story layer, and limited oak regeneration over the last half century (Abrams, 1992, 2003).

Although oak savannas are relatively less well understood than oak woodlands and forests, woody encroachment can lead to conversion of oak savannas into woodlands, representing a major compositional and structural modification (Bowles and McBride, 1998; Anderson et al., 2000; Nielsen et al., 2003). Research from various North American savanna ecosystems suggests that woody encroachment reduces system productivity (Hennessy et al., 1983) and biodiversity (Archer, 1995), and alters understory species composition (Anderson et al., 2000; Nielsen et al., 2003), making it important to understand options for reducing or ameliorating encroachment in oak savannas.

Unfortunately, little is known about restoring areas that have been encroached by woody vegetation. Some past work in oak woodlands and savannas has focused on reinstating understory

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fire regimes, with the goal of reducing woody encroachment through direct stem mortality (e.g., Anderson et al., 2000; Blake and Schuette, 2000; Franklin et al., 2003; Nielsen et al., 2003; Hutchinson et al., 2005). However, encroaching species have frequently been resilient to prescribed fires (Anderson et al., 2000; Franklin et al., 2003; Hutchinson et al., 2005; Albrecht and McCarthy, 2006), suggesting that reinstatement of this process alone might be ineffective in some situations (Nielsen et al., 2003). Potentially, these encroached ecosystems represent alternative stable states (Beisner et al., 2003), which may require thresholds, like understory fuel availability, to be surpassed before reintroduction of processes can be effective restoration measures (Suding et al., 2004).

Another option for restoring ecosystems degraded by woody encroachment is active removal of encroaching species. This approach might be successful in situations where encroachment has resulted in major structural alterations, such as canopy closure or development of midstory vegetation, which might inhibit the reestablishment of historic fire regimes (Sarr et al., 2004). Although active removal of encroaching woody vegetation has produced preliminary success in some conifer and aspen systems (Moore et al., 1999; Provencher et al., 2000; Jones et al., 2005), it is not known whether removing encroaching vegetation will restore historic regeneration dynamics (Allen et al., 2002). More research is needed, especially in understudied ecosystems such as oak savannas.

In this study, we used a series of experimental Midwestern oak savannas to evaluate the effects of mechanically removing encroaching mesophytic trees and large shrubs on woody species structure, composition, and regeneration. We quantified structure and species composition of the under-, mid-, and overstory before and for 3 subsequent years following removal of woody encroachment and compared these dynamics with encroached control sites. Furthermore, we investigated regeneration dynamics to determine whether removal of encroaching vegetation alters successional trajectory. If encroached savannas represent an alternative stable state, removed encroaching vegetation would be replaced by more encroachment by mesophytic species. Conversely, if treatments are successful over the timescale of this study, there should be little recruitment or recruitment by oak species, the pre-encroachment dominants (Karnitz and Asbjornsen, 2006). The results of this study will be valuable to land managers seeking to restore Midwestern oak savannas and will enhance fundamental knowledge of how ecosystems respond to woody encroachment removal.

2. Methods

2.1. Study system

Midwestern oak savannas historically formed the fire-maintained forest/prairie transition zone of North America (Nuzzo, 1986). These ecosystems are defined by a sparse oak overstory, which is encroached by mesophytic trees and shrubs within decades of fire suppression, and a dense herbaceous understory (Cottam, 1949; Curtis, 1959; Anderson, 1998). Less than 1% of Midwestern oak savannas remain intact and unencroached (Nuzzo, 1986); however, an unknown amount exists in an altered state degraded by woody encroachment. Efforts to restore heavily encroached savannas generally involve mechanical removal of encroaching trees, followed by prescribed understory fires (Packard, 1993; Nielsen et al., 2003).

2.2. Study area

We located eight savanna remnants (sites) along the western shore of Saylorville Lake (41°76′N, 93°82′W), a reservoir on the Des Moines River, near Des Moines, Iowa, USA. These sites ranged in size from 1.5 to 3.3 ha (Table 1) and were located on east/west oriented upland ridges, which are divided by valleys created by ephemeral streams. The predominant soil series at these sites are the Hayden (fine-loamy, mixed, superactive, mesic Glossic Hapludalf; developed under oak/hickory forest) and Lester (fine-loamy, mixed superactive, mesic Mollic Hapludalf; developed under oak savanna; Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions. Available URL: http://soils.usda.gov/soils/technical/classification/osd/index.html [accessed 30 September

Table 1
Description of study sites before and after mechanical removal of encroaching woody vegetation

Site	Size (ha)	Date of treatment	Dates of vegetation sampling	Study transect length (m)[a]	First season basal area (m^2/ha)[b]	Second season basal area (m^2/ha)[c,d]	First season canopy cover (%)[b]	Second season canopy cover (%)[c]
Restore 1	3.1	Winter 2002–2003	2002–2005	200	14.25	5.70	86.2	17.9
Restore 2	2.5	Winter 2002–2003	2002–2005	200	20.80	2.15	85.8	8.4
Restore 3	1.9	Winter 2003–2004	2003–2006	130	29.23	14.77	84.5	28.0
Restore 4	3.1	Winter 2003–2004	2003–2006	100	37.10	27.75	86.8	51.8
Control 1	2.1	N/A	2002–2005	180	21.28	21.33	83.7	87.0
Control 2	3.3	N/A	2002–2005	200	16.65	16.65	86.9	93.8
Control 3	1.5	N/A	2003–2006	105	27.52	27.43	83.7	85.1
Control 4	2.2	N/A	2003–2006	100	24.00	24.00	88.8	91.9

[a] Trees, saplings, shrubs, and seedlings were sampled in one 10 m wide nested belt transect/site.
[b] Pre-treatment values for sites undergoing restoration.
[c] Post-treatment values for sites undergoing restoration.
[d] Note: All trees were censused in the second season; however, DBH was recorded for new trees only.

2006]). Mean annual temperature, precipitation, and frost-free days for the city of Des Moines are 10 °C, 882 mm, and 133 (National Oceanic and Atmospheric Administration. Comparative Climate Data. Available URL: www.ncdc.noaa.gov [accessed 30 September 2006]). None of these sites have been plowed, but the landscape has a history of domestic grazing and has remained unmanaged since it was purchased by the U.S. Army Corps of Engineers, between 1965 and 1975 (Karnitz and Asbjornsen, 2006). Following Army Corps acquisition and removal of livestock, these sites were encroached by mesophytic trees (e.g., *Ostrya virginiana*, *Fraxinus americana*, *Ulmus americana*, *Ulmus rubra*; Karnitz and Asbjornsen, 2006). Pre-treatment canopy cover values ranged from 84 to 89% for control sites and 85 to 87% for treatment sites (assessed by hemispherical photographs; Table 1).

2.3. Encroaching woody vegetation removal

We removed encroaching woody vegetation from four of the eight study sites (restoration treatment), while the other four sites remained as unmanipulated controls. Restoration involved the removal of all non-oak stems >150 cm height, except at one site where we retained nut bearing species (i.e., oak, hickory, and walnut; see Asbjornsen et al., 2005; Brudvig and Asbjornsen, 2005). Encroaching trees and shrubs were cut by chain saws and burned in off-site slash piles by hand crews. The restoration treatment reduced basal area by 8.5–18.7 m^2/ha (Table 1). Post-treatment canopy cover values ranged from 85 to 92% for control sites and 8 to 52% for treatment sites (assessed by hemispherical photographs; Table 1). Canopy cover values for treated sites fall roughly within the range of published definitions for Midwestern oak savannas (10–50%: Curtis, 1959; 10–30%: Packard, 1993). Due to the amount of time needed to conduct these restorations (1–2 months/site) and the necessity for performing treatments during the winter to minimize soil impacts, we conducted the restoration treatment on two sites during winter of 2002–2003, and on the remaining two sites during the winter of 2003–2004 (Table 1). Although this resulted in two different study periods (see below), it may have made our study more robust by minimizing the influence of year effects (and thus increasing the importance of treatment effects).

2.4. Vegetation sampling

We used one nested belt transect/site to monitor species composition and densities of overstory trees, saplings, shrubs, and seedlings in the year before and for 3 years following treatments (Table 1). For four sites, the sampling period was 2002–2005 and for the remaining four sites we sampled from 2003 to 2006. Transects ran the length of each study area and ranged in size from 100 to 200 m, due to differences in the sizes of the eight savanna remnants (Table 1).

We sampled trees, defined as any living stem of at least 150 cm in height and 5 cm diameter at breast height (dbh; measured at 1.3 m), within a 10 m wide transect. We recorded species and dbh for all trees with base at least 50% within the transect. We sampled saplings in a 4 m wide transect, parallel to and centered on the middle of the tree transect. We recorded the species of each sapling, defined as any live woody stem taller than 1.5 m but less than 5 cm dbh. We sampled shrubs, defined as any woody plant stem, excluding vines, of at least 50 cm, but less than 150 cm in height, every 10 m in 3 m^2 plots, along the center of the tree transect. We tallied and recorded species for all shrubs with base originating from within the plot. For shrubs with multiple stems, we counted only the tallest stem. We recorded species for all seedlings, defined as woody stems less than 50 cm in height, in 1 m × 1 m plots, located every 10 m along the tree transect, at the transect center point. Seedling plots were also sampled for percent cover by understory vegetation (<50 cm in height), leaf litter, bare ground, and down woody material (DWM).

2.5. Data analysis

We used a three-tiered analysis to interpret impacts of removing encroaching woody vegetation on structure, composition, and regeneration dynamics in encroached and treated savanna remnants over the 4 year period of study. First, to understand structural changes, we used repeated measures analyses of variance (PROC GLM; SAS Institute, 2002), with site ($n = 4$) as the independent variable and year ($n = 4$) as the repeated effect. Dependent variables were the following mean values per site: percent ground cover by vegetation, leaf litter, bare ground, and DWM (assessed in 1 m × 1 m understory plots; see above), and total densities of the four vegetation size classes (individuals/ha). All dependent variables were log transformed prior to analysis, to normalize the residuals. No pre-treatment differences existed between treatment and control sites for any of the dependent variables (maximum $t = 3.40$, $p = 0.1149$; shrubs), so we considered impacts of the treatment significant at $\alpha < 0.05$ for the year × treatment interaction. To investigate how the removal treatment altered overstory trees of varying diameters, we used paired *t*-tests (treatment versus control sites) to compare tree densities in 10 cm intervals before and after treatment. Second, we used multi-response permutation procedure (MRPP; McCune and Mefford, 1999) to test for changes in composition between treatment and control areas. MRPP is a nonparametric test of the null hypothesis that no difference exists between predefined groups (McCune and Grace, 2002). We defined groups as treatment and control, ran MRPP for each size class (seedling, shrub, sapling, tree) and each year of the study, and considered treatment effects significant at $\alpha < 0.05$. The response variable was density of each occurring species (individuals/ha for seedling, shrub, sapling, and tree size classes). We used Sørensen distance as the MRPP distance measure to avoid the influence of outliers (McCune and Grace, 2002), since the woody vegetation removal treatment altered species composition and densities relative to control sites. Third, we investigated changes in individual species using repeated measures analyses of variance (PROC GLM; SAS Institute, 2002), with site ($n = 4$) as the independent variable and year ($n = 4$) as the repeated effect. Due to highly variable data sets including numerous zeros, the dependent variables were ranked densities (mean values per site) for the five most common species, plus *Quercus alba* (regardless of rank), in the seedling, shrub, and sapling size classes during each year of the study. We excluded trees from this analysis since there was little change in this stratum in years after treatment, which was selective to retain oaks (see above). Pre-treatment overstory tree composition is described in detail by Karnitz and Asbjornsen (2006).

3. Results

3.1. Structure

Relative to control sites, removal of encroaching woody vegetation increased percent cover by understory vegetation (year × treatment $F_{3,18} = 4.39$, $p = 0.0174$; Fig. 1a) and decreased cover by leaf litter (year × treatment $F_{3,18} = 4.56$, $p = 0.0152$; Fig. 1b) and bare ground (year × treatment $F_{3,18} = 4.86$, $p = 0.012$; Fig. 1c). There was no evidence for an impact on cover by DWM (year × treatment $F_{3,18} = 2.02$, $p = 0.1468$; Fig. 1d). Vegetation and leaf litter showed moderate changes 1 year following treatment, but transitioned dramatically in year 2 and retained these new levels 3 years following treatment (Fig. 1a and b). Conversely, bare ground decreased linearly throughout the 3 years following the restoration treatment (Fig. 1c).

Over the course of the study, we found no evidence that seedling densities differed between treatment and control sites (year × treatment $F_{3,18} = 1.07$, $p = 0.3881$; Fig. 2a). The restoration treatment altered shrub densities (year × treatment $F_{3,18} = 6.35$, $p = 0.004$; Fig. 2b), particularly in the second year after treatment, when densities were markedly increased in treatment sites. The restoration treatment initially reduced sapling densities (year × treatment $F_{3,18} = 18.41$, $p < 0.0001$; Fig. 2c); however, saplings returned to pre-treatment levels within 3 years (Fig. 2c). Tree densities were reduced by treatment and remained at new levels for the duration of the study (year × treatment $F_{3,18} = 98.72$, $p < 0.0001$; Fig. 2d).

No differences existed between treatment and control sites for any of the 10 cm tree size class intervals prior to treatment (all p-values > 0.17; Fig. 3). Tree removal reduced stem densities for smaller size classes (5–10 cm: $t = 20.47$, $p < 0.0001$; 10–20 cm: $t = 2.91$, $p = 0.0269$; 20–30 cm: $t = 3.06$, $p = 0.0222$; 30–40 cm: $t = 1.97$, $p = 0.0965$); however, little or no change occurred for size classes >40 cm (40–50 cm $t = 1.00$, $p = 0.3559$; 50–60 cm: $t = 1.66$, $p = 0.1482$; 60–70 cm: no change; >70 cm: no change; Fig. 3). Tree size class distributions at control sites remained relatively unaltered following treatment, with minor changes occurring due to low levels of recruitment and/or mortality (Fig. 3).

3.2. Composition

No pre-treatment differences existed in species composition for seedling (MRPP; $A = -0.0036$, $p \approx 0.51$), shrub ($A = 0.0014$, $p \approx 0.43$), sapling ($A = 0.054$, $p \approx 0.099$), or tree size classes ($A = 0.011$, $p \approx 0.34$). Following the restoration treatment, we found no differences in any years for seedlings (year 1: $A = -0.0097$, $p \approx 0.53$; year 2: $A = -0.012$, $p \approx 0.46$; $A = -0.043$, $p \approx 0.79$). Shrub composition remained unaffected for 1 year following treatment and then differed in years 2 and 3 (year 1: $A = 0.077$, $p \approx 0.08$; year 2: $A = 0.16$, $p \approx 0.023$; $A = 0.18$, $p \approx 0.013$). Sapling composition did not differ in years 1 and 2 following treatment; however, there was some evidence

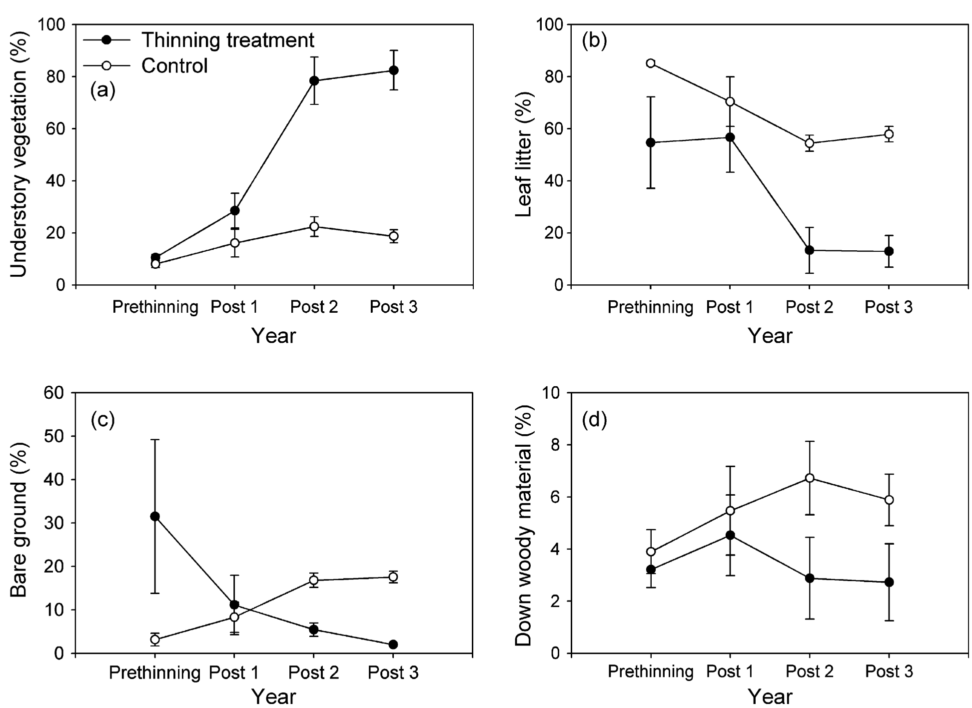

Fig. 1. Cover by understory vegetation (a), leaf litter (b), bare ground (c), and down woody material (d) in oak savannas 1 year prior to and 3 years following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Circles represent site means ± 1S.E.

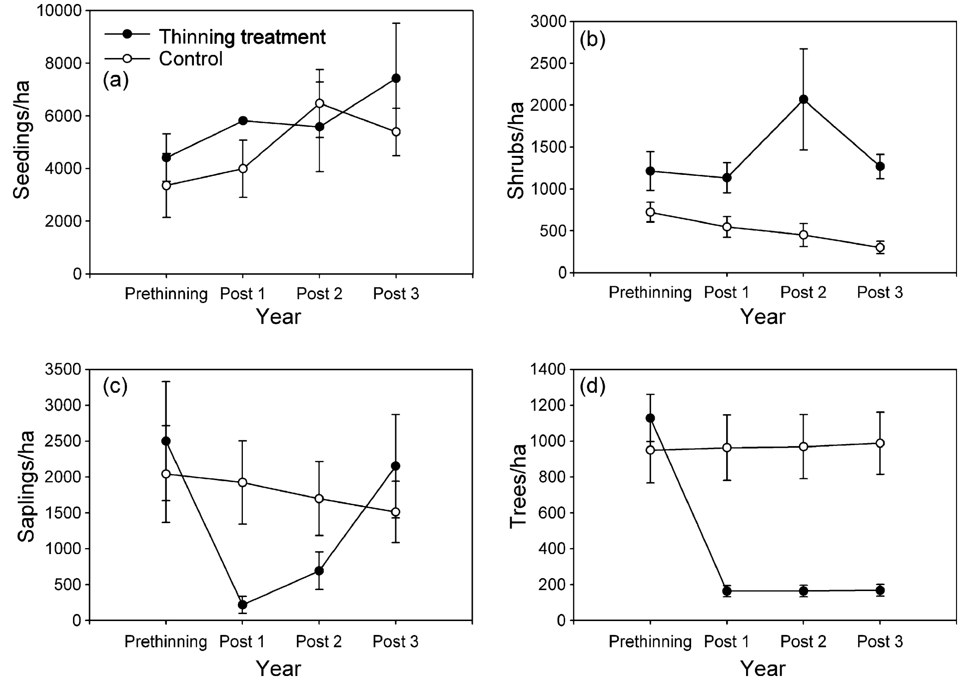

Fig. 2. Seedling (a), shrub (b), sapling (c), and tree densities (d) in oak savannas 1 year prior to and 3 years following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Circles represent site means ± 1S.E.

for a difference in year 3 (year 1: $A = 0.021$, $p \approx 0.19$; year 2: $A = 0.051$, $p \approx 0.08$; $A = 0.066$, $p \approx 0.068$). Tree composition differed between treatment and control sites during all years following treatment (year 1: $A = 0.15$, $p \approx 0.0094$; year 2: $A = 0.19$, $p \approx 0.0071$; $A = 0.18$, $p \approx 0.0064$).

3.3. Regeneration dynamics

None of the common species in the seedling size class were significantly affected by the restoration treatment (all *p*-values > 0.18). However, seedlings in treatment sites displayed one of three general trends, relative to seedlings in control sites: (1) no response (e.g., *O. virginiana*, *F. americana*; Fig. 4), (2) an increase in abundance 1 year after treatment, followed by a return to pre-treatment levels in years 2 and 3 (e.g., *U. americana*, *Prunus serotina*, *U. rubra*; Fig. 4), and (3) a gradual increase in abundance during the 3 years of study following the restoration treatment (e.g., *Q. alba*; Fig. 4).

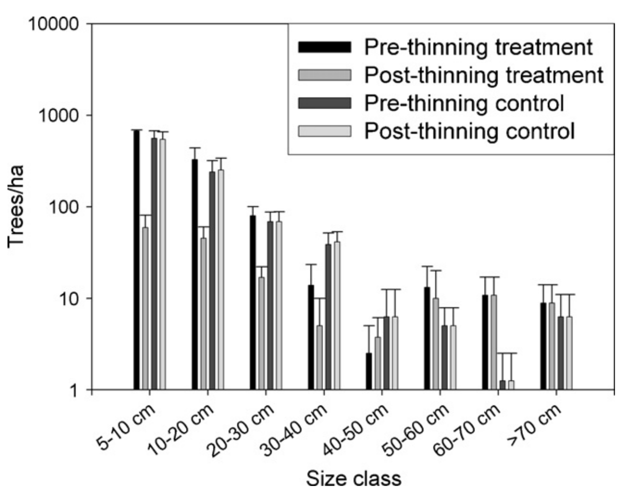

Fig. 3. Tree size classes in 10 cm intervals in oak savannas prior to and following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Bars represent site means ± 1S.E. Note log scale on vertical axis.

None of the common species in the shrub size class were significantly affected by the restoration treatment (all *p*-values > 0.16). However, shrubs displayed one of three general trends following encroachment removal: (1) no response (e.g., *F. americana*, *Ribes missouriense*, *Q. alba*; Fig. 5), (2) an increase in abundance 2 years after treatment, followed by a return to pre-treatment levels in year 3 (e.g., *Cornus racemosa*, *O. virginiana*; Fig. 5), and (3) a gradual increase in abundance during the 3 years of study following treatment (e.g., *Symphoricarpos orbiculatus*; Fig. 5).

The restoration treatment significantly impacted sapling densities of *O. virginiana* (year × treatment $F_{3,18} = 9.67$, $p = 0.0005$), *C. racemosa* (year × treatment $F_{3,18} = 6.29$, $p = 0.0042$), and *F. americana* (year × treatment $F_{3,18} = 3.42$, $p = 0.0395$), with each species displaying a decrease in abundance 1 year after treatment, followed by a return to pre-treatment levels by year 3 (Fig. 6). In addition, saplings displayed one of two general trends following encroachment removal: (1) no response (e.g., *Q. alba*; Fig. 6), or (2) sustained declines over the course of the study (e.g., *Acer nigrum*, *Carya ovata*; Fig. 6).

4. Discussion

4.1. Structure and composition

Our study of woody encroachment removal in oak savannas produced mixed results for structure and composition. The treatment reduced overstory tree density, due to removal of

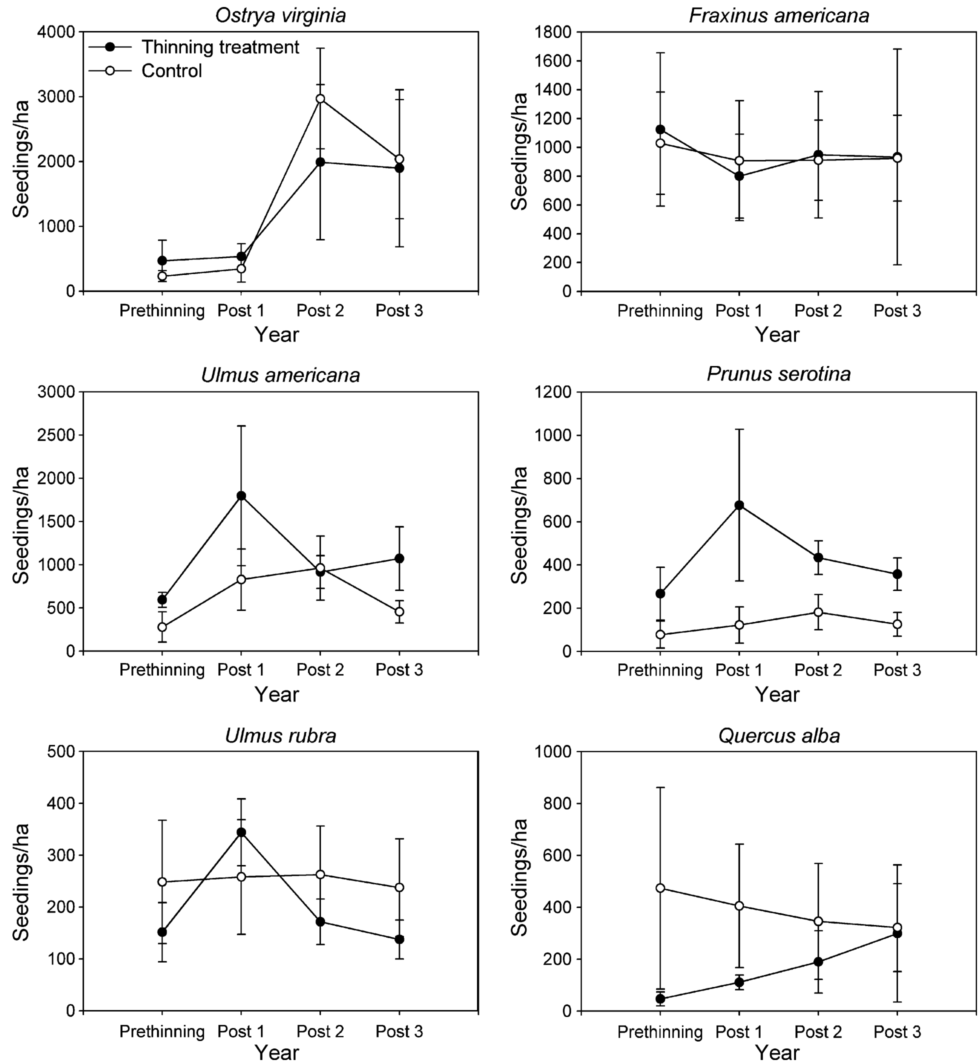

Fig. 4. Seedling (stem height < 50 cm) densities for common species and *Q. alba* (overstory dominant) in oak savannas 1 year prior to and 3 years following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Circles represent site means ± 1S.E.

trees in smaller size classes, and altered overstory tree composition in favor of *Quercus* spp. However, initial alterations to the regenerating strata did not persist for the duration of this study. Although sapling densities of encroaching species were reduced by the treatment, these returned to pre-treatment levels by the end of the study. Shrub densities increased 2 years after restoration, before returning to pre-treatment levels (see Section 4.2). Furthermore, regeneration was dominated by encroaching mesophytic species, while *Quercus* spp. recruitment was largely unaffected by restoration (see below). Some of our results, such as alterations to shrub and sapling species composition were not apparent until 2–3 years after treatment implementation (see Section 4.2), underscoring the importance of long-term monitoring during savanna restoration (Magnuson, 1990).

In general, research with canopy thinning and prescribed fire in oak ecosystems has produced variable impacts on stand structure and composition. Several studies have demonstrated sustained effects of prescribed fire and/or canopy thinning on understory structure and composition (Ward, 1992; Arthur et al., 1998; Blake and Schuette, 2000; Hutchinson et al., 2005), while others have found impacts, if any, to be short-lived (e.g., Franklin et al., 2003; Albrecht and McCarthy, 2006; Stan et al., 2006). The relatively few studies that have found impacts of management treatments on overstory structure and composition have either employed long-term use of prescribed fire alone (e.g., Peterson and Reich, 2001) or mechanical tree removal followed by understory fires (Brose et al., 1999). The application of fire-alone may be followed by mortality of encroaching species only after a substantial time lag, whereas combined use of canopy thinning and fire may help to expedite this process. Conversely, results from conifer-encroached systems suggest that mechanical removal-alone might effectively restore structure and composition (e.g., Provencher et al., 2000; Sarr et al., 2004; Jones et al., 2005).

4.2. Regeneration dynamics

Individual species responses to the restoration treatment were variable. Although mechanical removal reduced shrubs and saplings for several invading species (e.g., *A. nigrum*, *C. ovata*), advanced regeneration (sapling size class) was

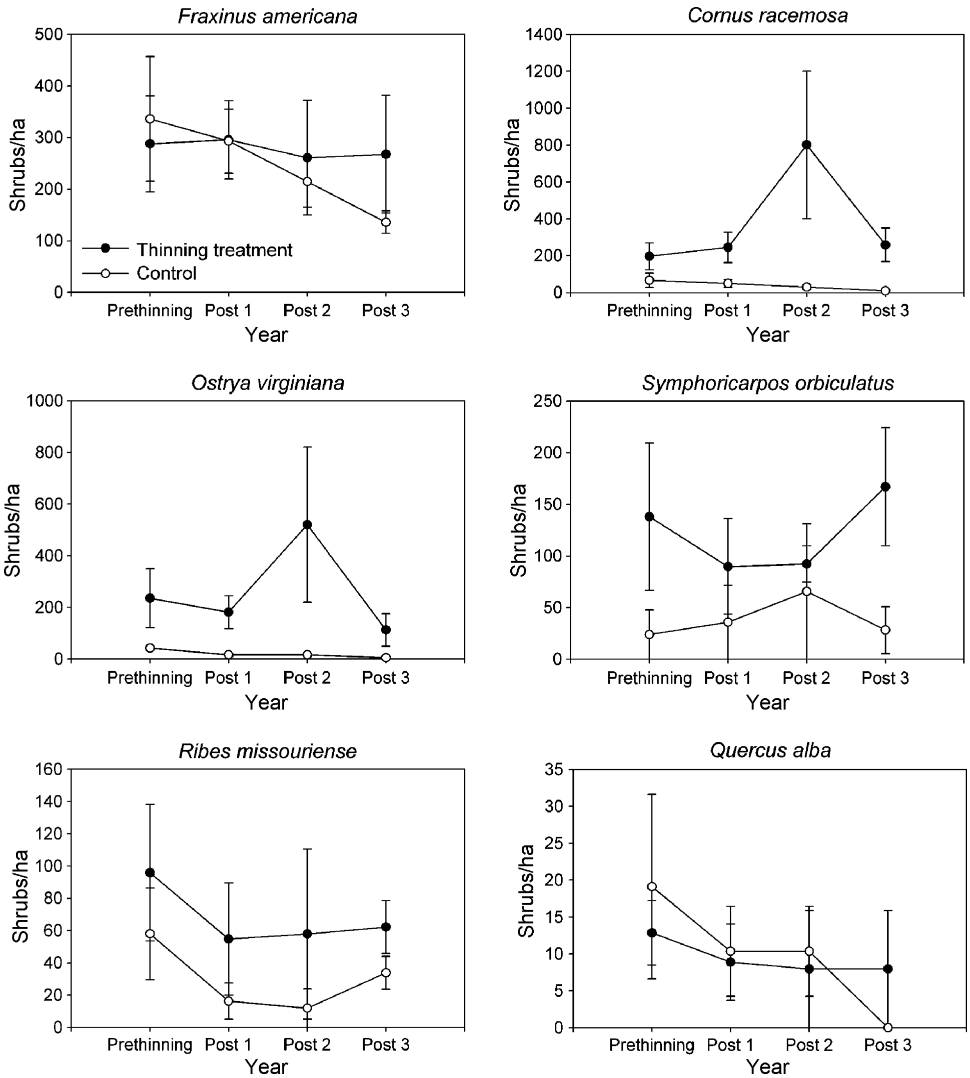

Fig. 5. Shrub (stem height 50–150 cm) densities for common species and *Q. alba* (overstory dominant) in oak savannas 1 year prior to and 3 years following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Circles represent site means ± 1S.E.

characterized by reduction followed by vigorous reestablishment. This was part of a recruitment pulse that proceeded through the shrub and sapling strata, with increased respective densities 2 and 3 years following removal of encroaching woody vegetation. The species-level data reveal that this was driven by the common encroaching species *O. virginiana* and *C. racemosa* (and to a lesser extent, *F. americana*), whose responses to the treatments closely mirrored those of the shrub and sapling data. This result helps to explain the delayed divergence in species composition in the shrub and sapling layers (2 and 3 years after treatment, respectively). While these two species reestablished, many other encroaching species did not, thus, altering community composition. Similarly, Albrecht and McCarthy (2006) found that selective removal of invading *Acer rubrum* trees in southern Ohio oak forests had only temporary effects as *A. rubrum* returned to pre-treatment levels within 4 years of removal. Stump resprouting, rather than establishment from seed, was the dominant means of advanced regeneration in our study. *C. racemosa* seedlings were rare in all years and *O. virginiana* seedlings did not increase in density until 2 years after treatments (presumably from a mast seeding event, as this pattern was present at all sites). However, both species dramatically increased as shrubs 2 years after treatments and as saplings 1 year later. *O. virginiana* is a vigorous stump resprouter (Preston and Braham, 2002) and *C. racemosa* rapidly spreads in high-light environments via clonal growth (Boeken and Canham, 1995).

Despite a trend of increased *Q. alba* seedling densities following the restoration treatment, advanced regeneration was dominated by non-*Quercus* species. This is contrary to Ward (1992), who found canopy thinning to be a useful technique for promoting oak regeneration in Connecticut oak woodlands. Past work at our sites demonstrated that removal of encroaching vegetation produced positive growth of *Q. alba* seedlings 1 year after treatment (Brudvig and Asbjornsen, 2005). Our current findings, however, suggest that this might be insufficient when compared to the vigorously regenerating competing species (e.g., *C. racemosa*, *O. virginiana*). Competition by tall understory vegetation, especially saplings of mesophytic tree species, can limit oak regeneration in Midwestern woodlands

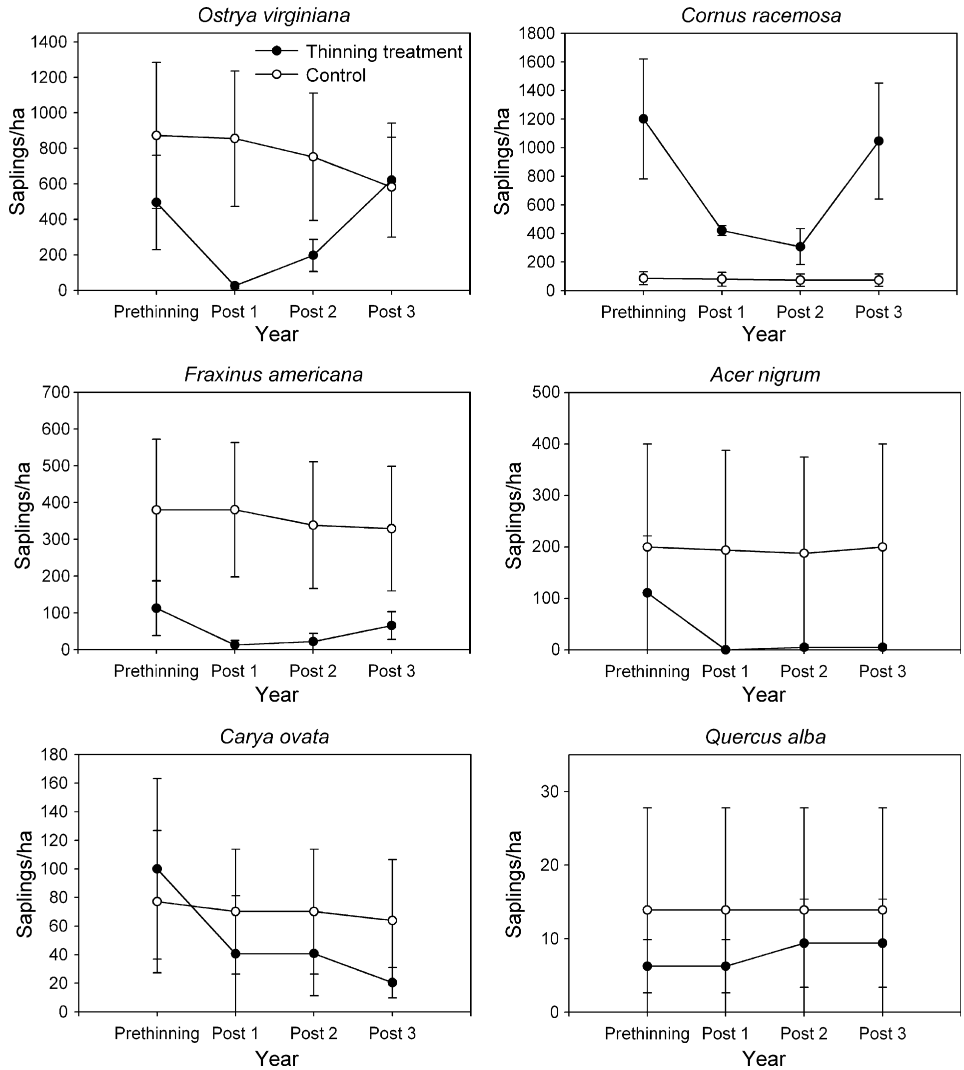

Fig. 6. Sapling (stem height > 150 cm, DBH < 5 cm) densities for common species and *Q. alba* (overstory dominant) in oak savannas 1 year prior to and 3 years following removal of encroaching woody vegetation (thinning treatment; $n = 4$) and at control sites ($n = 4$). Circles represent site means ± 1S.E.

(Lorimer et al., 1994). More research is needed to better elucidate the role of savanna restoration for promoting oak regeneration in light of the full regenerating community.

4.3. Alternative stable states in oak savannas

Our results support the existence of an alternative stable state in the oak savannas in this study, whereby stand trajectories continue toward canopy replacement by encroaching species despite removal efforts. A similar result was found by Albrecht and McCarthy (2006) in Ohio oak woodlands, where tree removal and prescribed fire treatments were independently attempted. In both cases, encroaching species reestablished, while *Quercus* species were unaffected. Anderson et al. (2000) described an Illinois oak savanna resilient to management by prescribed fire after several decades of fire suppression. They attributed this to reduced fire intensity following heavy establishment by *Salix humilis*. In our study, sapling densities returned to pre-treatment levels within 3 years following the restoration treatment. This stratum was dominated by encroaching species, while *Q. alba* saplings were unaffected and represented only a minor component of the sapling stratum in all years except 1 year following restoration. Although we found that changes in the tree stratum persisted throughout the duration of our study, rapid sapling recruitment suggests that tree densities will return to pre-treatment levels within several decades. The overstory will eventually be dominated by non-*Quercus* species. Thus, site trajectories appear to be directed toward reestablishment of a dense canopy layer, rather than persistence of the desired open-canopy condition (Asbjornsen et al., 2005).

In terms provided by Frelich and Reich's (1998) boreal forest models, our savanna sites may be explained by the 'discontinuous change' model, if there is a threshold in disturbance intensity that must be surpassed before the system will convert from mesophytic woodland to oak savanna. Alternatively, if these sites are better explained by the 'continuous change' model, this suggests that repeated disturbance will be necessary to maintain these sites as savanna, as the successional trend will always be toward the later-successional mesophytic woodland

(Abrams, 1992). However, choosing the correct model may be further complicated, as Frelich and Reich (1998) suggest that certain disturbances may be cumulative. In our study, removal of 48–92% of the tree canopy did not alter the path of succession. However, it is possible that repeated tree removal, or tree removal followed by prescribed fire, may additively represent a severe enough disturbance to surpass a threshold necessary to alter system trajectory away from closed canopy woodland and toward the desired broken canopy oak savanna state. The topic of alternative stable states is well suited to work with restoration (Suding et al., 2004) and future study with savanna systems is warranted.

4.4. Management implications

Although woody encroachment removal successfully accomplished some desirable management outcomes (Asbjornsen et al., 2005), such as promoting dense understory cover and reestablishing overstory structure and composition, we suggest that future research with prescribed fire will be necessary to identify long-term management options for controlling encroaching woody vegetation and promoting oak regeneration at these sites. Although initial savanna encroachment can take several decades (Bowles and McBride, 1998; Karnitz and Asbjornsen, 2006), this study demonstrates that reestablishment of encroachment vegetation following removal is quite rapid due to stump resprouting. Mechanical removal and/or fire may have to be reimplemented frequently (e.g., <every 5 years) to effectively control encroaching woody vegetation. Alternately, herbicide application following mechanical removal might be explored as a tool to reduce stump resprouting.

In addition to overstory impacts, treatments influenced understory fuels in this study. Although the restoration treatment increased understory vegetation cover, which is desirable in savannas as this stratum represents an important fuel source (Asbjornsen et al., 2005), it decreased leaf litter, which also serves as fuel for understory fires. The consequences of these changes for oak savanna fire regimes and resulting restoration implications warrant future study. Development of understory vegetation (fuels) may represent an important threshold that must be surpassed during restoration before fires can become sufficiently intense to produce stem mortality in encroaching trees and shrubs (Nielsen et al., 2003).

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