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The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas

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Summary

1. Savannas throughout the world are characterized by spatial gradients of resources created by scattered overstorey trees. These gradients are important for maintenance of understorey biodiversity; however, they may be disrupted by woody encroachment, resulting in alterations to understorey vegetation. Little is known about the status of understorey gradients in encroached savannas, or whether they redevelop during restoration and if so, by what mechanism.

2. We used a large-scale restoration experiment with Midwestern oak savannas (USA) to address these issues. We established understorey transects radiating from overstorey *Quercus alba* L. trees to inter-canopy gaps in four control and four restoration treatment sites. Along each transect, we sampled understorey vegetation over three field seasons and we recorded physical factors in the final year of study.

3. Restoration produced a strong relationship between visible sky (e.g. light penetrating to the understorey) and distance from overstorey trees, while none existed in control sites. Restored sites had greater variability in soil moisture due to higher levels immediately after rain at all distances from trees, coupled with greater drying rates, particularly at farther distances from overstorey trees. With restoration, a positive relationship between cover by understorey vegetation and distance from overstorey trees developed and strengthened over time, whereas no relationship existed in control sites. Cover by each of the major functional groups, forbs, graminoids, and woody species, contributed to this pattern. Furthermore, after restoration, species richness increased with distance from overstorey trees in the final year of study.

4. Nonmetric multidimensional scaling (NMS) showed that common understorey species were correlated with gradients of canopy cover and soil moisture, which were associated with restoration plots, and gradients of soil texture and N, which were associated with both restoration and control plots. Furthermore, restoration strengthened correlations between NMS plot scores and distance from overstorey trees.

5. *Synthesis and applications.* Re-establishing overstorey structure was an important step during restoration of the oak savannas in this study. While encroached savannas contained a homogenized understorey, restored sites contained understorey patterning typical of intact savannas. The timeframe for re-establishment – within years of restoration, after decades of degradation – demonstrates high resiliency and suggests restorability of other highly degraded sites; however, we recognize the importance of prescribed fire for maintaining open savanna structure and, probably, promoting further understorey pattern development.

Key-words: canopy thinning, community assembly, gradient analysis, Midwestern oak savanna, *Quercus alba*, restoration, woody encroachment removal

Introduction

Temperate and tropical savannas are characterized by scattered overstorey trees, which produce spatially variable understorey resources and spatially organized understorey plant communities (Belsky *et al.* 1989; Scholes & Archer 1997; Breshears 2006). Canopy trees intercept precipitation and solar radiation and alter soil biogeochemistry, resulting in modified microenvironments under trees relative to inter-canopy gaps. This arrangement in understorey resources

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might be best conceptualized as gradients aligned from overstorey tree boles to inter-canopy gaps. Furthermore, understorey plants align along savanna resource gradients, resulting in different plant communities beneath savanna trees, relative to those in inter-canopy gaps (e.g. Belsky *et al.* 1989; Ko & Reich 1993; Ludwig *et al.* 2004). The implication can be exceptionally high levels of biodiversity in savannas, making them important conservation targets (e.g. Belsky *et al.* 1989; Leach & Givnish 1999). However, savannas throughout the world have been encroached by woody species over the last century, due to a combination of fire suppression, overgrazing, and climate change (Archer, Scifres & Bassham 1988; Abrams 1992; Scholes & Archer 1997; Bustamante *et al.* 2006). Woody encroachment has increased tree density and canopy cover in savannas (Scholes & Archer 1997) and has altered the levels and distributions of understorey resources (Breshears 2006). Although these changes may be accompanied by alterations to understorey vegetation, this has not been well investigated beyond forage species (Scholes & Archer 1997). Efforts to mechanically remove woody encroachment have taken place in numerous savanna ecosystems and understanding how these alter the spatial arrangement of understorey resources and vegetation will be critical to successful savanna restoration (Breshears 2006).

To guide savanna restoration, two important questions need to be resolved. First, what is the status of understorey resource and vegetation gradients in encroached savannas? This will help evaluate the potential for restoring encroached savannas and set a baseline by which restoration success can be evaluated. Secondly, how do trees influence understorey resources and vegetation after woody encroachment has been removed? This will assess important components of restoration success: physical environment, community structure, and ecosystem function (SER 2004) and will have implications for restoring high levels of biodiversity. In this study, we answer these two general questions with a large-scale oak savanna restoration experiment in Iowa, USA. This experiment involves savanna remnants that are either encroached by woody vegetation or have had all encroaching woody vegetation mechanically removed. Inter-canopy gaps are filled with trees in encroached sites, whereas restored sites have scattered overstorey trees interspersed among inter-canopy gaps. Thus, this represents an ideal experiment in which to test for restoration of savanna gradients.

To guide analyses, we provide a series of hypotheses about gradients in encroached and restored savanna remnants. In restored savannas, understorey light levels and soil moisture after rainfall will increase with distance from overstorey trees (Belsky *et al.* 1989; Ko & Reich 1993; Breshears *et al.* 1998), due to reinstatement of canopy openings. Conversely, we hypothesize that gradients of understorey light levels and soil moisture after rainfall will be weak in encroached savannas, where inter-canopy gaps have filled with trees. Furthermore, rates of soil drying will be greatest in inter-canopy gaps of restored savannas, due to increased solar levels (Belsky *et al.* 1989; Jackson *et al.* 1990; Ludwig *et al.* 2004). Levels of soil nutrients and soil organic matter are generally greater below savanna tree canopies (e.g. Belsky *et al.* 1989; Jackson *et al.* 1990; Ko & Reich 1993; Ludwig *et al.* 2004) and restoration may re-establish these gradients; however, we do not predict that this will happen during the timeframe in this study (2–3 years). Gradients of soil nutrients and organic matter are dampened in encroached savannas, due to homogenization of nutrient distributions (Hibbard *et al.* 2001), and we predict a disruption of these gradients in encroached sites.

Understorey vegetation in savannas is particularly well suited to understanding how restoration alters plant communities over time, as communities are dominated by herbaceous species (Leach & Givnish 1999; Meisel, Trushenski & Weiher 2002) and reorganization can occur over time-scales as short as several years (Brudvig in press). We expect cover by understorey vegetation to increase with distance from overstorey trees in restored sites (Scholes & Archer 1997) and for this pattern to be driven by graminoids, which can dominate inter-canopy gaps in Midwestern oak savannas (Leach & Givnish 1999; Meisel *et al.* 2002). Conversely, we hypothesize that understorey vegetation will display similar cover at all distances from overstorey trees in encroached sites. We hypothesize that soil texture will be important for plant community patterns; however, past work suggests that this operates among sites, rather than within sites (Leach & Givnish 1999; Meisel *et al.* 2002), and thus, we do not expect to find gradients of soil texture in our study, nor do we expect restoration to influence soil texture over our time-scale. We do, however, hypothesize understorey vegetation to be spatially organized along gradients of understorey light, soil moisture, and soil nutrients (Belsky *et al.* 1989; Leach & Givnish 1999; Ludwig *et al.* 2004; Meisel *et al.* 2002), some of which may be influenced by overstorey trees in restored sites.

Materials and methods

STUDY SYSTEM

Midwestern oak savannas are defined by a broken (predominantly oak) overstorey and a continuous, highly diverse understorey dominated by forbs and graminoids (Nuzzo 1986; Leach & Givnish 1999). Although widespread prior to Euro-American settlement, encompassing an estimated 10–13 million ha in central North America, Midwestern oak savannas now occupy <1% of this range due to agricultural conversion or fire suppression that has led to woody encroachment and conversion to woodlands (Nuzzo 1986). To restore oak savannas to the Midwestern landscape, restoration efforts frequently target encroached remnants by first mechanically removing encroaching woody vegetation and later re-establishing an understorey fire regime (Packard 1993).

Midwestern oak savannas are ideal for understanding impacts of woody encroachment and removal. They historically formed the fire-maintained transition zone between North American prairies and deciduous forests; however, due to fluctuations in climate, this zone has varied in size and position during the last 10 000 years (Clark *et al.* 2001). Thus, the region occupied by Midwestern oak savannas naturally exhibits periods of woody encroachment (conversion to woodland) and encroachment removal (conversion to savanna or prairie).

SITE DESCRIPTION

This study is part of a large-scale restoration experiment with Midwestern oak savannas in Iowa, USA (Asbjornsen *et al.* 2005). In 2002, we established eight research sites containing *Quercus alba* savanna remnants along the western shore of Saylorville Lake, a US Army Corps of Engineers reservoir (41°76′ N, 93°82′ W). Sites varied in size from 1·5–3·3 ha (Brudvig & Asbjornsen 2007) and had a history of ~100 years of cattle grazing, which terminated following Army Corps purchase between 1965 and 1975 (Karnitz & Asbjornsen 2006). After purchase, the land was unmanaged and woody species encroached the savannas over the next several decades [e.g. *Ostrya virginiana* (Mill.) K. Koch, *Fraxinus americana* L., *Ulmus americana* L.; Karnitz & Asbjornsen 2006]. None of the sites have been ploughed. Soils are a mixture of the Hayden (Glossic Hapludalf; developed under oak/hickory woodland) and Lester series (Mollic Hapludalf; developed under oak savanna; USDA 2007). Mean annual temperature, precipitation, and frost-free days for the city of Des Moines are 10 °C, 882 mm, and 133 days (NOAA 2007).

To restore the historically sparse, oak-dominated overstorey (described by historic land survey notes; Asbjornsen *et al.* 2005), half of the sites were randomly selected for a restoration treatment, where all encroaching trees and large shrubs (height > 1·5 m) were cut with chain saws, removed from the sites, and burned in slash piles (Brudvig & Asbjornsen 2007). No herbicides were applied to stumps of cut stems. We conducted the restoration treatment at four of eight sites during the winters of 2002–2003 and 2003–2004. The treatments were only conducted during winter to minimize soil impacts; 2 years were thus needed to treat all four sites. We retained the remaining four sites as untreated controls.

Indicators from the over- and understorey vegetation suggest that the restoration treatment has been initially successful. The restoration treatment reduced canopy cover from 84–89% to 8–52%, while canopy cover in control sites remained between 84% and 92% (Brudvig & Asbjornsen 2007). Values at treatment sites fell roughly within those published for Midwestern oak savannas (Packard 1993). The restoration treatment reduced basal area from 14–37 m^2 ha^{-1} to 2–27 m^2 ha^{-1}, whereas control site basal area was between 16 and 27 m^2 ha^{-1} prior to and following treatment (Brudvig & Asbjornsen 2007). The restoration treatment significantly altered overstorey composition in favour of *Quercus* species (Brudvig & Asbjornsen 2007) and regeneration rates for *Q. alba* were increased by the restoration treatment (Brudvig & Asbjornsen 2008). Three years after treatment, understorey species richness had increased by 225% in treatment sites, resulting in post-treatment values of 14–21 species m^{-2}, compared to 8–11 species m^{-2} in control sites (Brudvig in press). The number of savanna plant species in treatment sites increased over time, with 19 common species (present in ≥ 10% of permanently marked understorey plots) representative of savanna flora 3 years after treatment (Brudvig in press).

VEGETATION SAMPLING

In 2004, we randomly selected five large, open-grown *Q. alba* trees (canopy radius > 6 m) on level uplands at each site. For each tree, we estimated the distance from the bole to the canopy edge (see Brudvig & Asbjornsen 2005) and established a randomly oriented transect radiating from the bole to 1·5× the distance to the canopy edge. In instances where transects oriented toward another oak tree, we selected a different random direction. Along each transect, we established a 1 × 1-m permanently marked understorey plot, with the first plot adjacent to the tree, resulting in between five and 6 plots per transect. We also established a permanently marked 1 × 1 m ‘gap’ plot located at 3× the distance to the canopy edge, in the same random direction as the under-canopy transect. Between July 2004 and August 2006, vegetation was sampled annually in each of the 241 plots. During each census, we recorded species and estimated cover for all understorey plants (woody plants < 50 cm height including re-sprouts and all herbaceous plants) originating from within the plot. We also estimated total cover by vegetation, leaf litter, bare soil, and down woody material.

PHYSICAL GRADIENT SAMPLING

We collected hemispherical photographs at 1·5 m above each understorey plot during cloudless early morning hours of July 2006. We used a Coolpix 900 camera and 270° fisheye lens, levelled and oriented so the plane of the film faced north. Photographs were analysed with HemiView Canopy Analysis Software Version 2·1 (Delta-T Devices Ltd 1999, Cambridge, UK) to determine the percentage of visible sky (inverse of canopy cover).

In July 2006, we collected a soil sample for each understorey plot. Each sample was a composite of eight sub-samples from the area immediately surrounding each plot (one sub-sample from each plot corner and one from the midpoint of each plot side), taken with a 1·9 cm diameter soil probe to 10 cm. Each sample was analysed 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 sent to Ward Laboratory (Kearney, NE, USA) and analysed for pH, % organic matter (OM), and concentrations of nitrate N, total P, and K.

To understand patterns of surface soil drying, we sampled soil moisture to a depth of 10 cm in the centre of each understorey plot with a theta probe (Delta-T Devices Ltd, Cambridge, UK) during four time periods in 2006 (26–28 April; 15–19 May; 2–6 June, 4–8 July). Sampling time periods were 5 consecutive days without rain, following a rainfall of > 0·6 cm. The first sampling period was shortened to 3 days due to a second rain storm.

STATISTICAL ANALYSES

We defined understorey gradients as significant linear relationships between variables of interest and distance from overstorey trees. To test for spatial structuring of vegetation and physical factors by overstorey trees, we constructed multiple linear regression models, except for soil moisture, which was tested using two-way repeated analysis of variance (ANOVA). We evaluated five stepwise linear regression models, each fitting a series of permanent plot variables against distance from overstorey tree, by treatment (PROC REG, SAS 2002). We retained variables in the final models based on $P < 0·05$. A model of understorey physical factors included percentage of visible sky, soil pH, OM, N, P, K, and the percentages of sand, silt, and clay for each permanent plot. A model of ground cover variables included percentage of cover in permanent plots by vegetation, leaf litter, bare ground, and down woody material in each of the 3 years of study. A model of understorey cover-by-functional group included the percentage of cover in permanent plots by forbs, graminoids, and woody species in each year of study. A model of understorey species diversity included species richness, Simpson’s diversity, Simpson’s dominance, and species evenness for each permanent plot in each year of study (Magurran 2004). A model of understorey richness-by-functional group included richness of forbs, graminoids, and woody species in permanent plots, in each year of study. To test for differences in levels of soil moisture, we used repeated measures split-plot ANOVA (PROC GLM; SAS 2002), with treatment (main plot effect) and distance from overstorey tree (split plot effect) as dependent variables, days 1–5 of the sampling periods as the repeated effect, and the mean soil moisture (by day) recorded during the four sampling periods as the independent variable.

To determine the extent to which plant communities were structured by understorey physical gradients, we used nonmetric multidimensional scaling (NMS) in PC-ORD (McCune & Mefford 1999). The first matrix was 2006 cover values for the 44 species occurring in ≥ 5% of plots (common species). The second matrix contained the following plot-level environmental variables: % visible sky, soil pH, OM, N, P, K, % sand, % silt, % clay, and minimum, maximum, and average recorded soil moisture. We used Sørensen distances with a random starting configuration on 40 runs with real data, each with 400 iterations, and a stability criterion of 0·00001. We selected the number of dimensions in the final solution based on further dimensions reducing stress by < 5 (McCune & Grace 2002). To understand how overstorey trees structured understorey plant communities, we used linear regression (PROC REG, SAS 2002), comparing NMS plot scores and distance from overstorey trees, by treatment.

Results

PHYSICAL GRADIENTS

Visible sky, soil OM, pH, N, P, K, and texture

Distance from overstorey trees accounted for 25% of the variation in physical factors at treatment sites and 6% of the variation at control sites. In treatment sites, the percentage of visible sky increased with distance from overstorey trees (partial $r^2 = 0{\cdot}20$, $P < 0{\cdot}0001$; Fig. 1A) and soil pH decreased with distance from overstorey trees (partial $r^2 = 0{\cdot}05$, $P = 0{\cdot}005$; Fig. 1B). In control sites, soil K decreased with distance from overstorey trees ($r^2 = 0{\cdot}06$, $P = 0{\cdot}007$; Fig. 1C).

Soil moisture

There was an effect of sampling day on soil moisture, as soils dried for 5 days after rainfall (repeated measures ANOVA, test of day: $F_{4,\,152} = 3650{\cdot}44$, $P < 0{\cdot}0001$), and there were significant effects of day×treatment ($F_{4,152} = 455{\cdot}26$, $P < 0{\cdot}0001$), day×distance from overstorey tree ($F_{24,152} = 78{\cdot}83$, $P < 0{\cdot}0001$), and day×treatment×distance from overstorey tree ($F_{24,152} = 44{\cdot}10$, $P < 0{\cdot}0001$). Immediately after rain (day 1 in the drying period), soil moisture was greatest in canopy gaps at both treatment and control sites and lowest in plots adjacent to tree boles (Fig. 2). After rain, we observed greater soil moisture levels in treatment sites for all distances from overstorey trees, although this was less pronounced at positions closer to tree boles (Fig. 2). Soil moisture declined during drying periods more rapidly in treatment than in control sites, and by day 5, levels were lower in treatment sites at 0·5, 8·5, and 10·5 m from overstorey trees and in gap plots. In control sites across all days, the distribution of soil moisture across distances from overstorey trees was mildly hump-shaped, except for in gap plots, which always had the greatest levels (Fig. 2). In treatment sites, the day 1 distribution of soil moisture was progressively greater with distances from overstorey trees; however, a strong hump-shaped distribution developed by day 5 (Fig. 2).

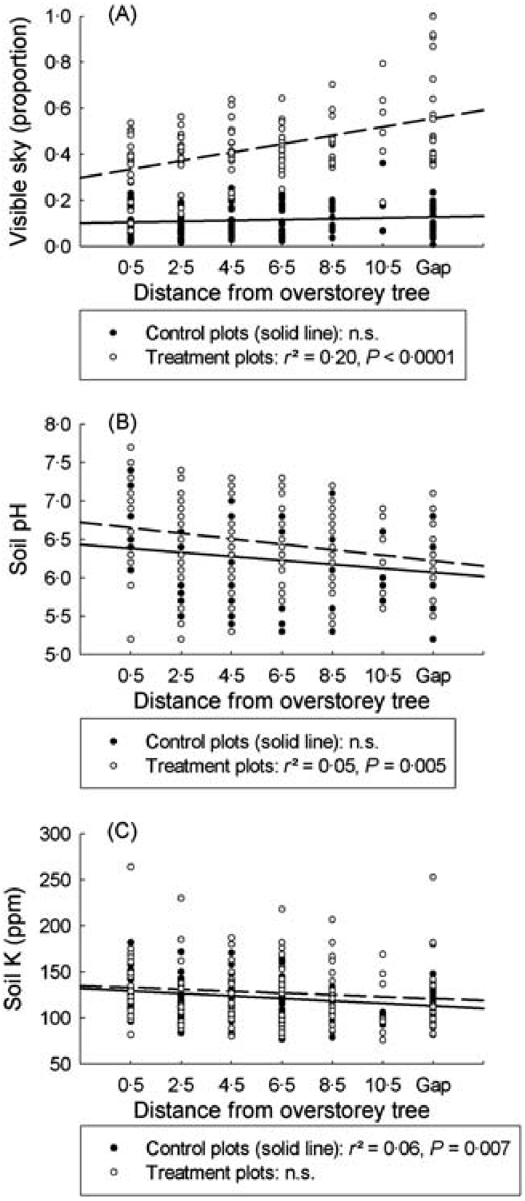

Fig. 1. Distribution of visible sky (A), soil pH (B), and soil K (C) in degraded (control) and restored (treatment) oak savannas. Plots were located at increasing distances from scattered overstorey trees and in inter-canopy gaps. Partial r^2 values are from multiple linear regression.

VEGETATIVE GRADIENTS

Cover variables

Distance from overstorey trees accounted for 48% of the variation in ground cover at treatment sites and 35% of the variation at control sites. In treatment sites, cover by vegetation increased with distance from overstorey trees in all years, with this correlation strengthening throughout the study (2004

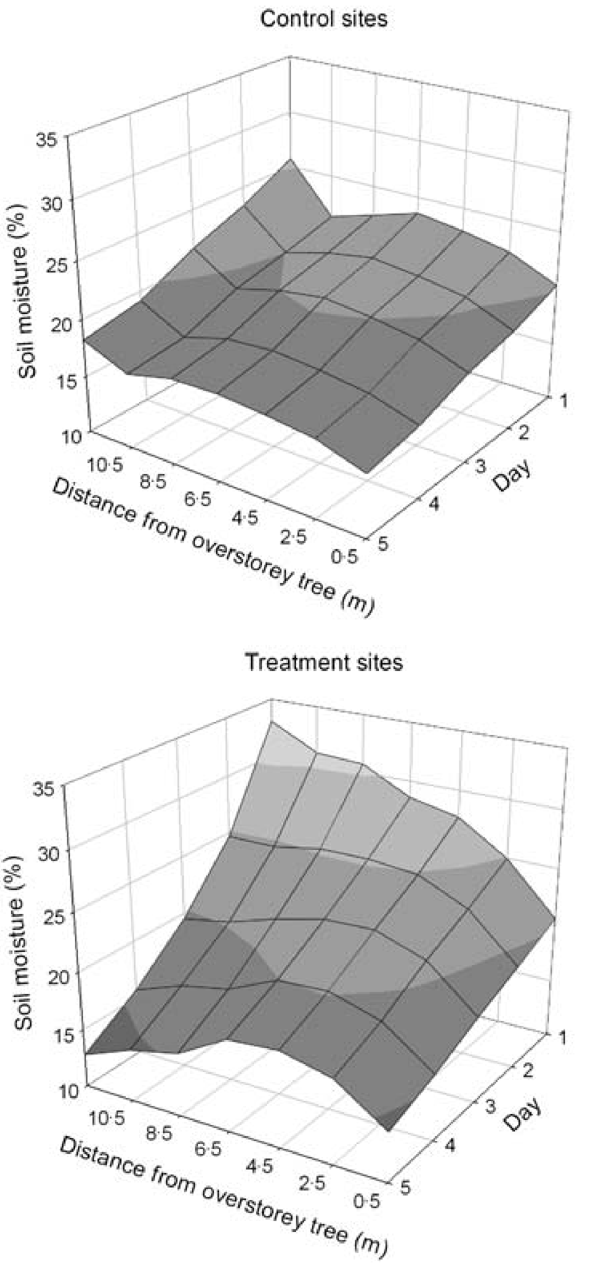

Fig. 2. Patterns of soil moisture (represented by the shaded contour planes) in degraded and restored oak savannas during 5-day drying periods, along transects from canopy trees to inter-canopy gaps.

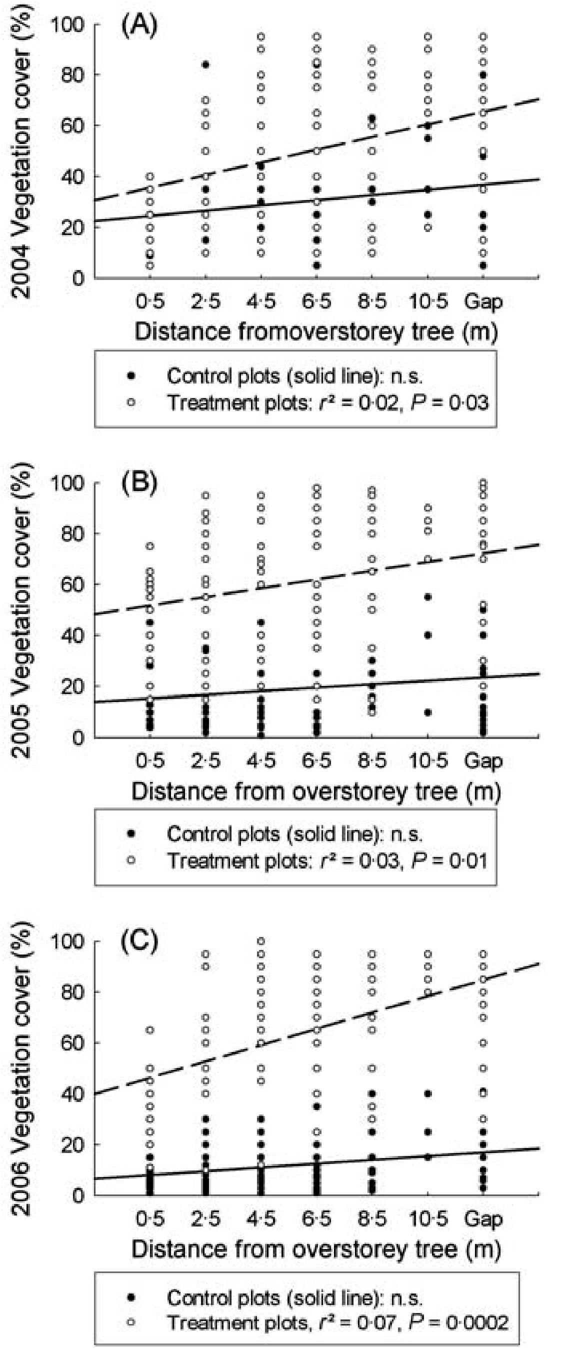

Fig. 3. Patterns of cover by understorey vegetation during 3 years of study in degraded (control) and restored (treatment) oak savannas. Plots were located at increasing distances from scattered overstorey trees and in inter-canopy gaps. Partial r^2 values are from multiple linear regression.

partial $r^2 = 0{\cdot}02$, $P = 0{\cdot}03$; 2005 partial $r^2 = 0{\cdot}03$, $P = 0{\cdot}01$; 2006 partial $r^2 = 0{\cdot}07$, $P = 0{\cdot}0002$; Fig. 3). Cover by down woody material decreased with distance from overstorey trees in 2004 (partial $r^2 = 0{\cdot}35$, $P < 0{\cdot}0001$). In control sites, cover by down woody material decreased with distance from overstorey trees in 2006 (partial $r^2 = 0{\cdot}29$, $P < 0{\cdot}0001$) and cover by leaf litter decreased with distance from overstorey trees in 2004 (partial $r^2 = 0{\cdot}06$, $P = 0{\cdot}001$).

Functional group cover

Distance from overstorey trees accounted for 33% of the variation in functional group cover at treatment sites and 8% of the variation at control sites. In treatment sites, 2005 cover by woody species (partial $r^2 = 0{\cdot}03$, $P = 0{\cdot}02$), and 2006 cover by forbs (partial $r^2 = 0{\cdot}04$, $P = 0{\cdot}008$; Fig. 4A), graminoids (partial $r^2 = 0{\cdot}12$, $P = 0{\cdot}0001$; Fig. 4B), and woody species (partial $r^2 = 0{\cdot}14$, $P < 0{\cdot}0001$; Fig. 4C) increased with distance from overstorey trees. In control sites, cover by woody species increased with distance from overstorey trees in 2006 ($r^2 = 0{\cdot}06$; Fig. 4C).

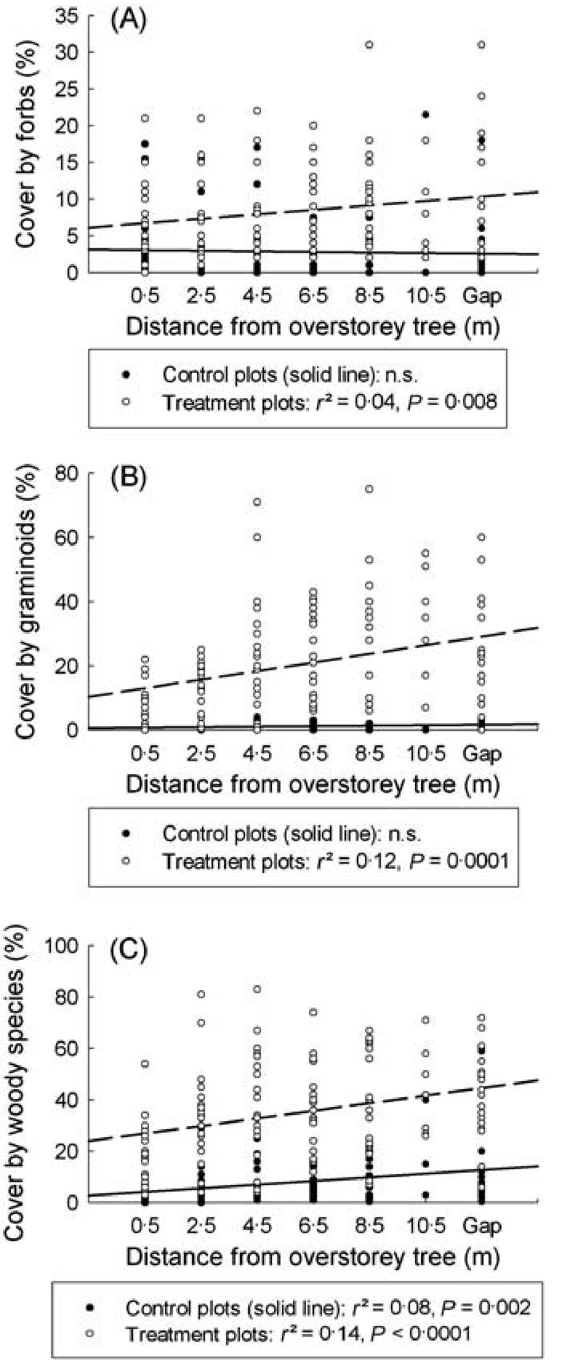

Fig. 4. Patterns of cover in 2006 by forbs (A), graminoids (B), and woody species (C), in degraded (control) and restored (treatment) oak savannas. Plots were located at increasing distances from scattered overstorey trees and in inter-canopy gaps. Partial r^2 values are from multiple linear regression.

Diversity variables

Distance from overstorey trees accounted for 11% of the variation in diversity variables at treatment sites and 4% of the variation at control sites. In treatment sites, species richness (partial $r^2 = 0{\cdot}05$, $P = 0{\cdot}02$) and Simpson's dominance (partial $r^2 = 0{\cdot}06$, $P = 0{\cdot}01$) increased with distance from overstorey trees in 2006. In control sites, species evenness decreased with

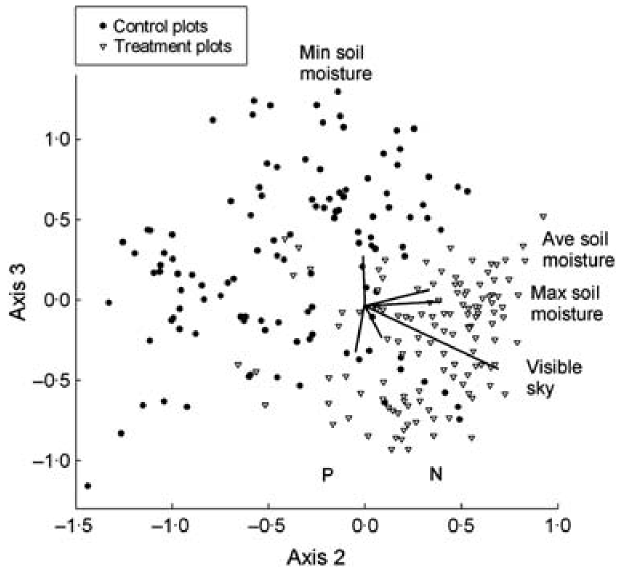

Fig. 5. NMS ordination of common understorey species (present in ≥ 5% of plots) for 241 plots in control (encroached) and treatment (woody encroachment removed) oak savannas. Vectors are scaled to show strength of correlations with axes. Axis 1 is related to soil texture, Axis 2 to canopy cover, and Axis 3 to soil drying.

distance from overstorey trees in 2006 (partial $r^2 = 0{\cdot}04$, $P = 0{\cdot}04$).

Functional group richness

Distance from overstorey trees accounted for 3% of the variation in functional group richness at treatment sites, but did not produce a significant model for control sites. In treatment sites, richness of woody species increased with distance from overstorey trees (partial $r^2 = 0{\cdot}03$, $P = 0{\cdot}04$).

NONMETRIC MULTIDIMENSIONAL SCALING

The final three-dimensional solution had a stress value of 21·55. In sum, the three main axes accounted for 62·6% of the variation in plant species data and each axis produced a stress score that was significantly lower than chance, based on Monte Carlo tests with 50 runs of randomized data (Axis 1, 2, 3: $P = 0{\cdot}0196$). Axis 1 accounted for 18·2% of the variation and was positively associated with % visible sky and % sand and negatively associated with N, % clay, minimum soil moisture, and average soil moisture (Table 1). Axis 2 accounted for 24·1% of the variation and was positively associated with % visible sky, N, K, maximum soil moisture, and average soil moisture (Table 1). Axis 3 accounted for 20·2% of the variation and was positively associated with % silt, minimum soil moisture, and average soil moisture and negatively associated with % visible sky, pH, OM, N, P, and % sand (Table 1). Treatment and control plots were divided along Axes 2 and 3. Treatment plots were generally associated with positive values along Axis 2 and negative values along Axis 3, while the reverse was true for control plots (Fig. 5). Treatment and control plots were distributed across positive, negative,

Table 1. Pearson correlations (r) between environmental variables and nonmetric multidimensional scaling axes for common species in Midwestern oak savannas along gradients from tree boles to inter-canopy gaps (n = 241). Significant correlations are in bold. Axis 1 is related to soil texture, Axis 2 to canopy cover, and Axis 3 to soil drying

	Axis 1		Axis 2		Axis 3	
Variable	r	P (one-tailed)	r	P	r	P
% visible sky	0·21	**0·0006**	0·54	**< 0·0001**	–0·42	**< 0·0001**
Soil pH	–0·073	0·13	0·088	0·087	–0·15	**0·010**
Soil organic matter	–0·078	0·11	0·058	0·19	–0·18	**0·0023**
Soil nitrate N	–0·18	**0·0025**	0·19	**0·002**	–0·29	**< 0·0001**
Soil P	–0·065	0·16	–0·096	0·069	–0·31	**< 0·0001**
Soil K	–0·10	0·059	0·11	**0·043**	–0·11	0·052
Soil % sand	0·15	**0·011**	–0·066	0·15	–0·23	**0·0002**
Soil % silt	–0·087	0·089	0·052	0·21	0·21	**0·0005**
Soil % clay	–0·16	**0·008**	0·043	0·25	0·073	0·13
Min. soil moisture	–0·18	**0·0021**	–0·054	0·20	0·32	**< 0·0001**
Max. soil moisture	–0·11	0·050	0·43	**< 0·0001**	0·055	0·20
Mean soil moisture	–0·14	**0·016**	0·39	**< 0·0001**	0·15	**0·011**

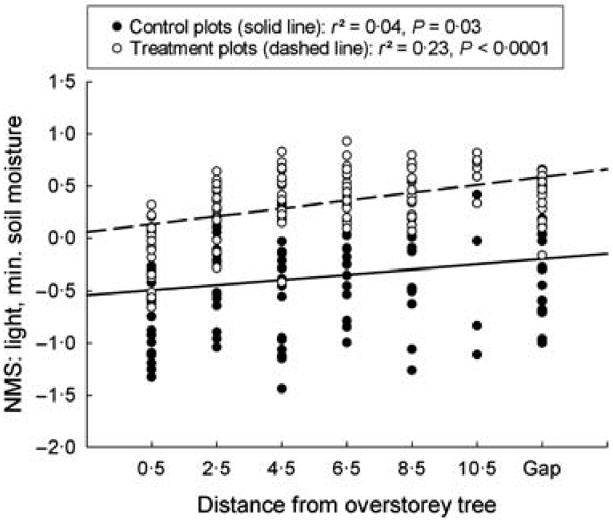

Fig. 6. Results of linear regression for common understorey species NMS Axis 2 plots scores along transects from tree boles to inter-canopy gaps in degraded (control) and restored (treatment) oak savannas.

and neutral values along Axis 1 (data not presented). Axis 1 plot scores were not correlated with distance from overstorey trees for treatment (r^2 = 0·002, P = 0·57) or control plots (r^2 = 0·01, P = 0·23). Axis 2 plot scores increased with distance from overstorey trees for treatment (r^2 = 0·23, P < 0·0001) and control sites (r^2 = 0·04, P = 0·03; Fig. 6). Axis 3 plot scores were not correlated with distance from overstorey trees for treatment (r^2 = 0·004, P = 0·49) or control plots (r^2 = 0·007, P = 0·36).

Discussion

Woody encroachment removal (i.e. restoration) had important implications for understorey spatial patterns in the savannas in this study. Although trees were generally not important for spatial organization in encroached savanna remnants, restoration produced or dramatically strengthened a number of understorey resource and vegetation gradients, which were organized around scattered overstorey trees.

UNDERSTOREY PHYSICAL GRADIENTS

Following restoration, overstorey trees influenced spatial patterns of visible sky and spatio-temporal distributions of surface soil moisture. Spatially variable understorey light levels are a hallmark of savannas (Breshears 2006), while spatial and temporal variability in soil moisture levels were described by Ko & Reich (1993) for Midwestern oak savannas and pastures and by Breshears *et al.* (1997) for semi-arid piñon/juniper woodlands. We further established the importance of restoration for producing patterns of soil moisture previously predicted in simulation studies (Breshears *et al.* 1998; Caylor, Shugart & Rodriguez-Iturbe 2005), and observed in non-encroached savannas (Belsky *et al.* 1989; Jackson *et al.* 1990; Ludwig *et al.* 2004). Immediately after rainfall, restored sites had greater soil moisture levels and this was most pronounced in inter-canopy gaps, which may be due to decreased canopy interception (Breshears *et al.* 1998; Caylor *et al.* 2005). However, soil moisture levels decreased most rapidly in inter-canopy gaps of restored sites, leaving restored and control site values similar after 5 days. Potentially, this was due to higher evaporation rates resulting from increased levels of solar radiation in restored sites (Breshears *et al.* 1998; Caylor *et al.* 2005). Interestingly, after 5 days of drying, a hump-shaped distribution of soil moisture developed, with levels greatest in intermediate distances from trees. Anderson, Brumbaugh & Jackson (2001) found that spatial and temporal alterations to soil moisture by savanna trees limited herbaceous understorey productivity, but facilitated *Prosopis glandulosa* seedling survival. Furthermore, Asbjornsen *et al.* (2007) determined that an *Ulmus*-encroached oak savanna displayed higher stand transpiration rates and strikingly lower water tables than a site with encroachment removed. Thus, our findings may have implications for patterns of understorey productivity and regeneration dynamics as well as site water balances in restored savannas.

We found little evidence for spatial patterns of soil nutrients, in the encroached or restored savannas in our study. Hibbard *et al.* (2001) demonstrated alterations to many soil properties within 50–77 years of woody encroachment in grasslands. It is unclear whether the < 40 years of encroachment at our study sites was sufficiently long to alter soil biogeochemical patterns from the former savanna state. Furthermore, other studies have suggested that soil biogeochemistry is robust to change following up to 68 years of encroachment (McCarron, Knapp & Blair 2003; Hughes *et al.* 2006), suggesting that in some situations, savanna soil properties may persist long after the period of encroachment documented in our study. Long-term monitoring in our savanna restoration experiment will be necessary to fully understand the implications of restoration on savanna soil resource patterns.

VEGETATIVE GRADIENTS

Savannas are defined, in part, by a continuous (predominantly) herbaceous understorey (Scholes & Archer 1997), making impacts to this layer an important consideration during restoration. Following restoration, savanna trees influenced a gradient of understorey vegetation, with all three functional groups (forbs, graminoids, woody species) contributing to this pattern. As we predicted, graminoids were most dramatically influenced and showed a strong positive correlation with distance from overstorey trees by the end of the study. In general, productivity can increase under savanna trees, relative to inter-canopy gaps, during nutrient- or water-limited conditions, while shading and/or belowground competition by trees reduces understorey productivity when other resources are abundant (e.g. Callaway, Nadkarni & Mahall 1991; Belsky 1994; Scholes & Archer 1997). Using cover as a surrogate for productivity, our results suggest that the latter was true following restoration, which is in accord with past finding from mesic savannas (Scholes & Archer 1997). Conversely, in our control sites, only woody species contributed to the positive gradient in understorey vegetation, suggesting that major alterations to understorey structure have occurred after encroachment. These results are consistent with past findings that the encroached savannas in this experiment represent an alternative woodland state (Brudvig & Asbjornsen 2007).

Relatively few studies have considered patterns of species diversity in savannas. By the final year of study, we observed a modest positive correlation between species richness and distance from overstorey trees. This result supports Mlambo, Nyathi & Mapaure (2005), who found that species richness and diversity increased with distance from trees; however, our Simpson's diversity results did not follow this pattern. Species richness during the first 3 post-restoration years and Simpson's diversity in all years followed the pattern reported by Ko & Reich (1993) and Weiher (2003), who found richness to be similar under trees and in inter-canopy gaps. We found no support for the finding of Leach & Givnish (1999), who demonstrated that species richness peaked in low-to-moderately sunny microsites (hump-shaped distribution, with distance from tree). However, understorey cover changed dramatically at our sites over a relatively short time following restoration and species diversity may develop further during continued community assembly. Thus, continued monitoring will be important to test the effectiveness of restoration at producing patterns reported from non-encroached remnants.

CORRELATIONS BETWEEN PHYSICAL GRADIENTS AND VEGETATIVE GRADIENTS

Our NMS analysis suggested that understorey plant communities are reorganizing along resource gradients created by overstorey trees in restored, but not encroached sites. Axis 2 was most strongly correlated with % visible sky and maximum and average soil moisture, suggesting that this axis represents a gradient of canopy; as canopy cover decreases, visible sky directly increases, while maximum and average soil moisture increase via increased throughfall levels (supported by direct gradient analyses of soil moisture, above; Breshears *et al.* 1997, 1998). Furthermore, this canopy cover axis was more strongly correlated with distance from overstorey trees following restoration. This demonstrates two things: (i) light availability was important for determining understorey plant communities in degraded and restored oak savannas, and (ii) savanna trees were important for structuring plant community composition after restoration. These results are consistent with past findings from Midwestern oak savannas (Leach & Givnish 1999; Meisel *et al.* 2002); however, these studies also determined soil texture to be an important gradient, and we found only minor support for this (see below). The patterns we observed after woody encroachment removal are also consistent with past studies that found changes in species composition along direct gradients from tree boles to inter-canopy gaps (e.g. Belsky *et al.* 1989; Weltzin & Coughenour 1990) and between under-tree and inter-canopy gap environments (e.g. Ko & Reich 1993; Ludwig *et al.* 2004), providing support for this restoration methodology. We do recognize that our NMS analysis produced relatively high stress scores (McCune & Grace 2002); however, our results are nonetheless encouraging for an early stage in restoration. Furthermore, plant community–microenvironment correlations may strengthen as plant communities further assemble under the new conditions produced by restoration; however, at present it is unknown how future restoration activities, including prescribed fire to maintain the open structure produced by mechanical thinning, will impact assembly.

Axis 3 in the NMS analyses was related to soil drying. Per cent visible sky and % sand were negatively correlated with minimum soil moisture, suggesting that both solar-induced drying (Breshears *et al.* 1997, 1998) and percolation were important to this gradient. Treatment plots and control plots generally separated along this axis, suggesting that restoration had an impact on soil dryness and associated variables. Although minimum soil moisture appears to be important for understorey composition, this was not correlated with distance from overstorey trees. Axis 1 was also related to moisture; however, this appears to be mediated by a soil texture gradient. This axis was also related to N, presumably due to increased leaching rates in sandier microsites. Control and treatment plots were dispersed across this axis, suggesting that soil texture was not related to restoration (also supported by direct gradient analyses, above, which showed no impact of treatment on texture).

Conclusions

With regard to our initial questions, although we found evidence for some understorey spatial structure in encroached savannas, this was generally minimal. Thus, we conclude that following decades of encroachment, the savannas in this study were, by and large, devoid of characteristic understorey gradients. These data were nonetheless critical as baselines for evaluating restoration success in this study.

Trees were important for spatial organization of numerous understorey gradients, following woody encroachment removal. In particular, following restoration, trees influenced spatial patterns of cover by understorey vegetation, visible sky and soil moisture, which are characteristic of intact savannas (Breshears 2006). A gradient of canopy cover (associated with visible sky and soil moisture) was most strongly correlated with understorey community composition and with restored plots, suggesting that alterations to light and soil moisture might be important drivers of plant community change during restoration. However, understorey species were also associated with gradients of soil texture and N, which were associated with both treatment and control plots. The fact that several important gradients were re-established within years of restoration, after decades of degradation, demonstrates the resilience of these savannas. With understorey gradients universally strengthening over time, further strengthening of the correlations presented in this study is likely. If progressive strengthening continues over decadal time periods, gradient patterns at these sites may be restored to levels found in intact Midwestern oak savannas (e.g. Leach & Givnish 1999; Meisel *et al.* 2002). Thus, it appears that woody encroachment removal is an important step during Midwestern oak savanna restoration. However, implementation of prescribed fire will be critical for maintaining open canopy structure and allowing gradients to further develop. In the absence of fire, reinvasion by woody species is likely (Brudvig & Asbjornsen 2007). Since tree removal is used to restore encroached savannas worldwide (Scholes & Archer 1997), the results of this study provide support for a common restoration technique.

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