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ABSTRACT—Study areas in the Iowa Loess Hills were used to evaluate short-term responses of understory species to three treatment methods designed to facilitate restoration of *Quercus macrocarpa* savanna. Treatments included burning alone, burning with thinning, and burning with clear-cutting. Plant abundance and diversity were compared before treatment and one year after treatment. Ninety-nine plant species were identified during the study, of which 40 were new following treatment, although most of these were forest associates. Increases in diversity of understory species were observed after treatment, particularly in plots with combined burning and thinning. The forb group was most consistent in response to treatment, increasing in cover an average of 9% in burn-only plots to 33% in burn-clear plots. *Carex* spp. and *Eupatorium rugosum* were the species most consistently responsive to treatments, but responses varied widely among other species. Density of canopy tree species generally did not decline with burning, indicating fire alone is ineffective in short-term removal of established trees. Although short term, our results suggest that a combination of prescribed burning and thinning of canopy trees is most likely to provide environmental conditions suitable for increasing the amount and diversity of herbaceous species comparable to a savanna ecosystem, while also increasing fine-fuel loads that will facilitate future prescribed burning.

Key Words: bur oak, Iowa, Loess Hills, *Quercus macrocarpa*, restoration, savanna

INTRODUCTION

The Loess Hills region of western Iowa and Missouri is a distinctive landform extending north and south along the eastern bluffs of the Missouri River (Fig. 1; Bettis et al. 1986), with a similar formation found on the west bank of the Missouri River in Nebraska. Historically, the landform was dominated by either mixed-grass prairie or *Quercus macrocarpa* (bur oak) savanna (Mutel 1989; Rebertus and Burns 1997), both communities presumably maintained largely by periodic fire of natural or anthropogenic origin (Iffrig 1983; Stambaugh et al. 2006). Forests (canopy cover >50%) were limited either to more mesic southern portions of the Loess Hills or to protected areas along stream courses and sheltered slopes throughout the more northern Loess Hills (Curtis 1959; Roosa et al. 1986).

European settlement in the Loess Hills occurred circa 1843, with subsequent fire suppression allowing forest expansion from protected areas into surrounding prairie and savanna, and resulting in a decline and fragmentation of these grass-dominated ecosystems (Loomis and McComb 1944; Novacek et al. 1985; Bettis et al. 1986; Roosa et al. 1986; Anderson 1998; Brudvig and Asbjornsen 2005). This change included original *Quercus* savanna succeeding to *Quercus macrocarpa*–dominated forest, but ultimately, likely to be replaced by communities dominated by shade-tolerant species such as *Ostrya virginiana* (hop hornbeam) and *Celtis occidentalis* (hackberry) (Trecek-King 2003). By 1997, less than 1% of historic *Quercus macrocarpa* savanna remained throughout the Midwest (Nuzzo 1986; Rebertus and Burns 1997). Poor regeneration of *Quercus macrocarpa* in the extant Loess Hills forests also suggests future changes in plant community composition away from one dominated by *Quercus macrocarpa* (Russell and Fowler 1999; Abrams 2003; Brudvig and Asbjornsen 2005). Increases in woody cover over past decades are reported to be a significant factor in the decline of

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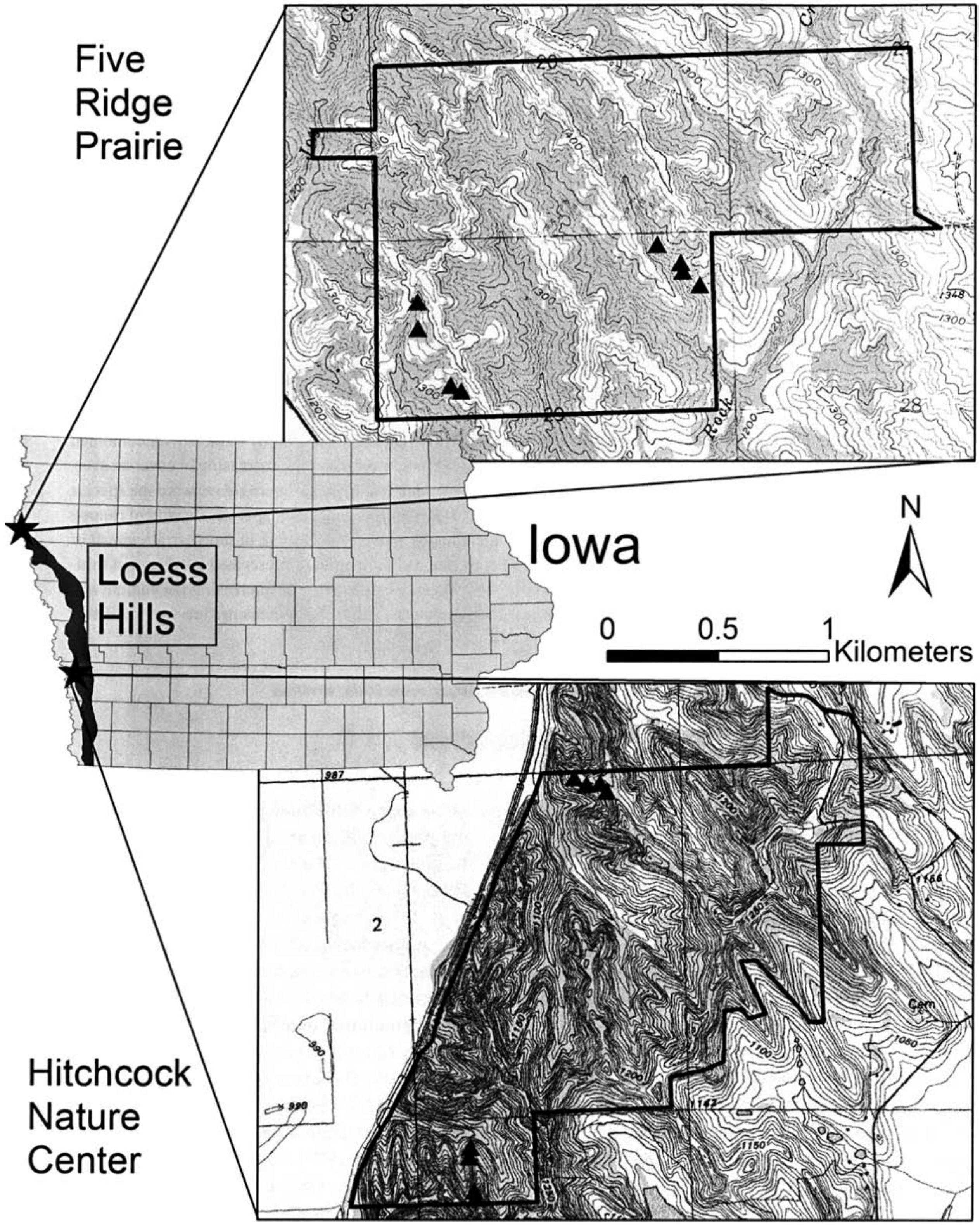

Figure 1. Location of Iowa's Loess Hills landform. The center map depicts Iowa with the Loess Hills outlined (darkened area) and study areas (stars) identified (modified from Novacek 1985). Topography, park boundaries, and the location of study sites within each park are depicted above (Five Ridge Prairie) and below (Hitchcock Nature Center). The scale bar is accurate for the park maps only, and the topographical scale interval in the park maps is in feet.

Loess Hills species. For example, 45 plant and animal species found in the Loess Hills are classified as rare in Iowa, with 21 of these on the Iowa list of threatened or endangered species (Mutel 1989).

From an ecological perspective, restoring and maintaining *Quercus macrocarpa* savanna in the Loess Hills is important to continuing regional biodiversity because savanna provides habitat for a unique species assemblage, as well as for species occurring in adjacent ecosystems (Anderson 1991; Grundel and Pavlovic 2008). To restore historic savanna and associated prairie plant communities, at least two strategies are available. One is to prevent further degradation of existing savanna ecosystems and the other is to reclaim areas lost to tree encroachment (Packard 1993; McCarty 1998; Brudvig and Asbjornsen 2005). The objective of our study was to assess treatment techniques by which to restore savanna, specifically in the Loess Hills of western Iowa. Here, we focus on initial, short-term effects of selective cutting and prescribed burning on the herbaceous community and understory woody-plant component of the current forest ecosystem. We intended to identify restoration techniques that would induce substantive changes in the understory plant community, leading to an increase in herbaceous savanna species, which would also constitute the fine fuels to facilitate future burns. Treatments were also expected to reduce woody-plant cover and create an environment more suitable to the regeneration of *Quercus macrocarpa* and prairie associates.

We focused on fire and mechanical removal of trees as the principal methods for savanna restoration. Fire is a natural process that can be used relatively efficiently in managing large grassland landscapes (e.g., Bragg and Hulbert 1976). It also is important to long-term survival and reproduction of *Quercus macrocarpa*, the dominant tree of the historic Loess Hills savanna (Aikman and Smelser 1938; Olson 1974; Perala 1974; Tinus 1980; Mutel 1989; Brudvig and Asbjornsen 2005). Mechanical tree removal was included in this study because in some systems fire alone has not proven successful in removal of established woody vegetation (White 1983; Packard 1993; McCarty 1998; Brudvig and Asbjornsen 2005). We expected the combination of fire and tree removal would induce greater change in both woody and understory species composition than would burning alone. However, we also expected the extremes in treatment (control and burning with clear-cutting) to result in plots that are structurally very different than that of the desired savanna of presettlement times.

METHODS

Study Areas

The study was conducted at two county parks in western Iowa: Five Ridge Prairie (42°40'N, 96°32'W) in Plymouth County in the northern Loess Hills, and Hitchcock Nature Center (41°24'N, 95°51'W) in Pottawattamie County, 140 km south of Five Ridge Prairie, near the center of the Loess Hills landform (Fig. 1). Native vegetation of much of Plymouth County at the time of settlement was short- to mixed-grass prairie on the uplands with *Quercus macrocarpa*–dominated forests and tallgrass prairie in the valleys (Aikman and Smelser 1938; Risser et al. 1981). Pottawattamie County to the south was generally described as tallgrass prairie with *Quercus macrocarpa* savanna on ridge tops and slopes and *Quercus macrocarpa–Carya cordiformis* (bitternut hickory) forest in low, protected areas (Aikman and Smelser 1938; Novacek et al. 1985; Rosburg and Glenn-Lewin 1996). Both study areas were historically savanna and thus were considered to have potential for successful restoration. Locations of historic savanna were indicated first by their topographic locations, then by the presence of large, open-grown *Quercus macrocarpa* within a matrix of smaller trees having comparatively pole-like boles. Further evidence is provided by historic accounts and artwork from the region (e.g., see Mutel 1989; Dillon et al. 2006). Conversion of the grasslands and savannas to woodland most likely occurred following European settlement in the region in the mid-1800s.

Soils of ridge tops at both study areas were predominantly Hamburg silt loams (Mesic Typic Udorthents) (Worster and Harvey 1976; Branham 1989). Soils of lower slopes at Hitchcock Nature Center also were Hamburg silt loams while those at Five Ridge Prairie were Castana silt (Mesic Entic Hapludolls). These are calcareous, silty soils of the Mollisol Soil Order that are well to excessively drained, with moderate permeability, and suited to establishment of *Quercus macrocarpa*. Climate of both study areas is continental, with hot summers and cold winters. July temperatures at Five Ridge Prairie and Hitchcock Nature Center average 23.3° and 23.5°C, respectively, while January temperatures average -8.8° and -7.1°C. Average annual precipitation is 67.4 cm at Five Ridge Prairie and 85.2 cm at Hitchcock Nature Center (MRCC 2009).

Study Sites

At each study area, two separate ridges with west- or southwest-facing slopes were selected as study sites and

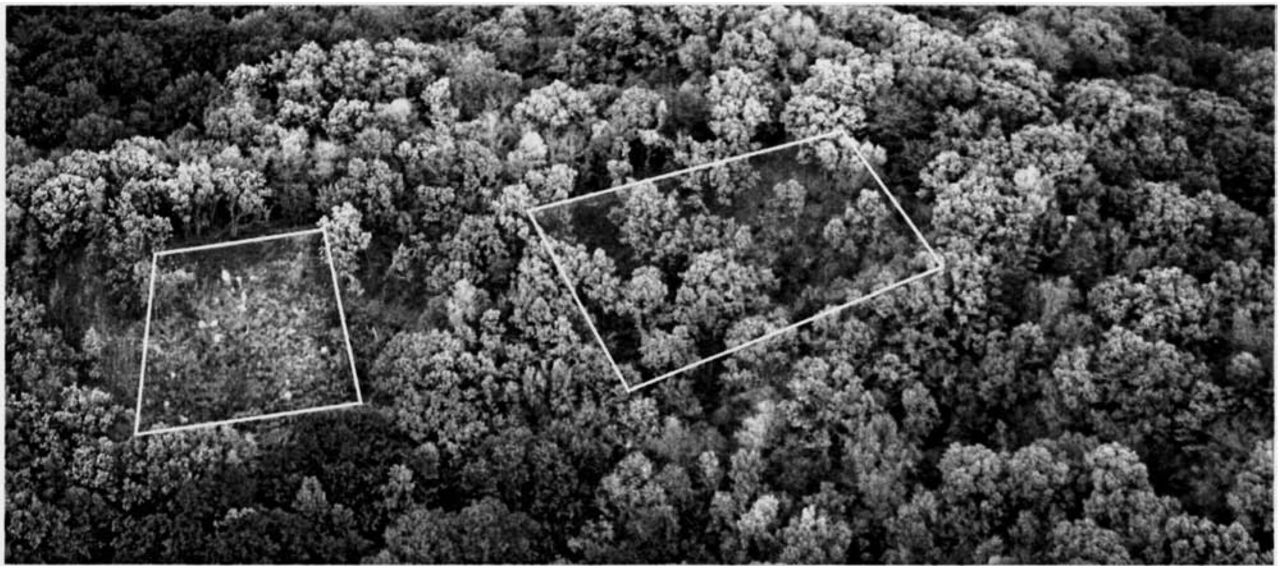

Figure 2. Photograph of the Loess Hills at Hitchcock Nature Center. The right square depicts post-treatment conditions in a burned and thinned plot (burn-thin), and the left square shows post-treatment conditions in a burned and cleared plot (burn-clear). The surrounding forest matrix is representative of what was once savanna but is now closed-canopy forests within this region. A burn-only plot is visible to the right of the burn-thin plot, but it is indistinguishable from the surrounding forest matrix.

designated Study Site 1 and Study Site 2. These four study site locations were selected because evidence suggested they recently supported savanna ecosystems. Evidence at Five Ridge Prairie consisted of small prairie remnants on ridge tops approximately 10–20 m upslope from the study plots. At Hitchcock Nature Center, large, widely scattered bur oak similarly suggested a one-time savanna (e.g., Phillips 2001). Each study site was divided into four treatment plots. All plots selected were characterized by nearly complete overstory canopy closure with each containing at least one mature *Quercus macrocarpa* (Fig. 2) (McKenzie 2006). Treatments were randomly applied to plots within each site. Treatment plot size varied from approximately 0.1 to 0.2 ha because of topographic variability.

Study plot treatments were as follows: control, in which neither burning nor tree removal occurred; burn-only, which involved burning but no tree removal; burn-thin, in which fire was applied and all woody plants over 1 cm diameter at breast height (dbh) except *Quercus macrocarpa* were removed; and burn-clear, in which all woody plants over 1 cm dbh were removed before the plot was burned. These treatments represented a range of intensities of tree removal from no change (control) to total alteration of forest overstory canopy (burn-clear). In some burn-thin plots, removal of some larger *Quercus macrocarpa* was necessary to achieve similar ground-level light intensities among plots (Anderson 1998; Meisel et al. 2002). Reduction in overstory canopy was intended to result in more xeric, high light surface conditions, that is, conditions under which both prairie species and *Quercus macrocarpa* seedlings preferentially regenerate (Bray 1960; Brudvig and Asbjornsen 2005; Royce et al. 2010).

Each burn treatment included a burned buffer of at least 10 m around each plot to simulate a broader-scale fire. It was necessary to conduct burns during winter to take advantage of greater available fuel from fall leaf-drop. Fire was expected to affect the herbaceous component of understory plants more than that of woody trees and shrubs. In particular, larger-diameter trees were unlikely to be affected by burning in the short term (Peterson and Reich 2001). Any response of smaller-diameter woody plants to initial burns might inform us to some extent about the efficacy of long-term treatment.

Treatment

Drip torches were used as the ignition source for the prescribed fires that occurred in each location. Average air temperature during the burns was 11.6ºC and average relative humidity was 40%. Because backing fires can burn more intensely than heading fires, backing fires were used to encourage greater fuel consumption.

At Hitchcock Nature Center, plots were burned during December 2003. Burning was patchy because of low fuel conditions. Clearing or thinning of plots was completed during January 2004. Downed trees were removed from plots and stems were painted with Tordon RTU (Dow

AgroSciences, Indianapolis, IN) to prevent resprouting. At Five Ridge Prairie, unsuitable weather and fuel conditions prevented burning during the winter of 2003–2004. Thus, plots were burned the next winter (December 2004). Even so, burns at Site 1 were patchy in the burn-thin plot and could not be carried out in the burn-clear plot because of unfavorable weather that continued throughout the winter and spring. While burn-thin and burn-clear plots at Site 1 were not adequately burned, tree removal treatments were applied, and these plots were included in the study. Clearing or thinning of plots at Five Ridge Prairie was completed during February and March 2005, and all cut material was removed. Unlike at Hitchcock Nature Center, however, cut stems at Five Ridge Prairie were not treated with herbicide. Even so, this did not result in a large amount of resprouting as noted in post-treatment sampling.

Sampling Procedure

Depending on topographic characteristics at the four study sites, treatment plots were separated by up to 300 m, with the corners of each permanently marked with metal poles and GPS coordinates recorded (McKenzie 2006). In the center of each treatment plot we marked a 10 × 10 m macroplot within which we recorded both the percentage of overstory canopy cover and the density of all woody plants with a diameter at breast height of greater than or equal to 1 cm. For the latter measurement we used a concave spherical crown densiometer after full leaf out.

To estimate understory cover, two parallel 21-m-long transects were established and permanently marked within each treatment plot. Along each transect, 10 systematically placed 1-m^2 (1 × 1 m) microplots (n = 20 microplots per plot) were evaluated for understory species and for cover groups using categories modified from Daubenmire (1959): >0%–1%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, 95%–99%, and >99% (McKenzie 2006). In addition to individual species cover, cover was also recorded for total cover, graminoids, forbs, woody species, litter, and bare soil. We defined understory species as those with individuals either not reaching breast height (1.4 m) or individuals with <1 cm dbh. Plant nomenclature follows the Great Plains Flora Association (1986).

Pre-treatment evaluations of both understory cover and woody species density were conducted during August 2003 at Hitchcock Nature Center and during August and September 2004 at Five Ridge Prairie. Post-treatment evaluations were conducted during July 2004 at Hitchcock Nature Center and during August and September 2005 at Five Ridge Prairie. Palmer Drought Severity Index values for the growing season preceding each sampling event were equal to 0 ± 1, suggesting that none were preceded by either extreme drought or extreme pluvial events.

Data Analysis

Understory cover data from transects within each treatment plot were averaged for analysis for each year. Statistically significant differences were set at 95% probability ($p \leq 0.05$), but these values can only be taken as trends because of the necessary use of pseudoreplication in these analyses. Pre-treatment and post-treatment understory cover of each species and cover group were compared using the Student's t-test (SAS Institute 1999; Minitab, Inc. 2003). A nonparametric one-way ANOVA was used to detect differences among treatment plots for each species (SAS Institute 1999). Where differences were significant, ANOVA was followed by a Student-Newman-Keuls multiple comparison test to identify differences among plots. Significant differences in Shannon diversity (H′) between sites were determined using a Student's t-test (Zar 1999). Although all species identified were included in our initial analyses, those presented in Tables 1–2 include only *Quercus macrocarpa* and species with an average cover of 5% or more in either sampling year for any treatment. For a full species list, see McKenzie (2006). Sample size was insufficient (n = 2) for statistical comparison among treatments for either woody plant density or overstory canopy. Thus, comparisons are shown either as the average density (number of stems/100 m^2) or as the percentage of overstory canopy cover.

RESULTS

Changes in Diversity and Richness

In total, 99 species were identified during the two years of the study: 76 at Five Ridge Prairie and 71 at Hitchcock Nature Center (McKenzie 2006). Forty species were recorded for the first time in Year 2, of which 16 were ruderal (r-selected) species such as *Erechtites hieracifolia* (fireweed) and *Chenopodium album* (goosefoot) (Great Plains Flora Association 1986). All tree species found in the overstory canopy were also present in the understory. Shannon diversity (H′) of understory species increased in all treated plots, although the increase was less at the northern sites (Five Ridge

TABLE 1
PERCENTAGE OF UNDERSTORY COVER AT FIVE RIDGE PRAIRIE STUDY SITES BY TREATMENTS FOR YEAR 1 (PRE-TREATMENT) AND YEAR 2 (POST-TREATMENT)

		Site 1					Site 2				
Cover groups	Year	Control	Burn-only	Burn-thin#	Burn-clear#	*F*-value	Control	Burn-only	Burn-thin	Burn-clear	*F*-value
Total cover	1^{τ}	69	67	76	76	0.1919	51	63	50	54	0.2973
	2	74	74	74	85	0.0619	51	54	55	80*	0.0001
Woody species	1^{τ}	67^{a}	48^{b}	75^{a}	70^{a}	0.0005	28^{b}	59^{a}	44^{a}	24^{b}	0.0001
	2	71^{a}	24^{c*}	45^{b*}	49^{b*}	0.0001	28^{a}	34^{c*}	30^{b}	16^{b}	0.0411
Graminoid	1^{τ}	4^{ab}	6^{ab}	1^{b}	6^{a}	0.0369	14^{ab}	8^{ab}	5^{b}	22^{a}	0.0066
	2	3^{ab}	3^{ab}	2^{b}	16^{a*}	0.0001	25^{ab}	14^{ab}	22^{b*}	58^{a*}	0.0001
Forbs	1	5^{ab}	23^{a}	4^{b}	7^{ab}	0.0001	13	10	3	17	0.0123
	2	4^{b}	42^{a*}	29^{a*}	51^{a*}	0.0001	4^{b}	10^{a}	16^{a*}	36^{a*}	0.0001
Bare soil	1	3	t	2	1	0.3143	3	4	t	9	0.1530
	2	2^{a}	13^{a*}	14^{a*}	2^{b}	0.0017	1^{a}	17^{a*}	7^{a*}	23^{b*}	0.0001
Litter	1	93	95	89	92	0.5987	96	91	97	91	0.2817
	2	92^{a}	82^{ab*}	75^{b*}	88^{a}	0.0094	97^{a}	66^{ab*}	81^{b*}	62^{a*}	0.0001

		Site 1					Site 2				
Woody species	Year	Control	Burn-only	Burn-thin#	Burn-clear#	*F*-value	Control	Burn-only	Burn-thin	Burn-clear	*F*-value
Celtis occidentalis	1^{τ}	25^{ab}	19^{b}	64^{a}	57^{a}	0.0001	3^{b}	22^{a}	17^{a}	2^{b}	0.0001
	2	21^{ab}	8^{b}	34^{a*}	24^{ab*}	0.0031	4^{ab}	5^{b*}	9^{a*}	1^{ab}	0.0022
Cornus drummondii‡	1^{τ}	42^{a}	26^{b}	9^{c}	10^{bc}	0.0001	t^{b}	8^{a}	3^{ab}	t^{ab}	0.0086
	2	41^{a}	9^{b*}	4^{c}	10^{bc}	0.0001	t^{a}	1^{b*}	2^{c}	t^{bc}	0.1061
Fraxinus pennsylvanica	1	8^{a}	t^{b}	t^{b}	3^{b}	0.0026	1^{b}	3^{ab}	4^{ab}	4^{a}	0.2245
	2	5^{a}	t^{b}	1^{ab}	1^{b}	0.0254	1^{a}	t^{b}	4^{ab}	1^{b*}	0.0165
Ostrya virginiana	1^{τ}	•	•	•	•	•	11^{c}	7^{ab}	3^{a}	1^{bc}	0.0763
	2	t	t	t	t	0.8198	7	6	7	t	0.0856
Parthenocissus spp.$^{\gamma}$	1	1	4	1	5	0.0776	5	2	4	7	0.6591
	2	1	2	2	9	0.0004	3	2	6	1	0.1859
Quercus macrocarpa	1	•	t	3	3	0.5433	•	3	•	•	0.3976
	2	t^{b}	0^{b}	3^{b}	8^{a}	0.0405	2^{b*}	3^{b}	t^{b*}	t^{a}	0.4435
Ribes missouriense	1	1	1	1	•	0.7121	•	•	t	t	0.2472
	2	t	1	t	1	0.6617	t	•	t	t	0.6547
Rubus occidentalis	1	2	1	1	4	0.1847	1	4	1	t	0.0224
	2	2	1	1	9	0.0287	2	3	4	t	0.3501
Symphoricarpos spp.‡$^{\gamma}$	1^{τ}	2	1	•	2	0.5169	t	•	t	t	0.7615
	2	1	t	t	2	0.2645	t	t	•	t	0.6547

Table 1 continued

		Site 1					Site 2				
Herbaceous species	**Year**	**Control**	**Burn-only**	**Burn-thin#**	**Burn-clear#**	***F*-value**	**Control**	**Burn only**	**Burn-thin**	**Burn-clear**	***F*-value**
Carex spp.	1^{τ}	2^{ab}	5^{ab}	t^{b}	5^{a}	0.0686	8^{ab}	4^{b}	3^{b}	15^{a}	0.0188
	2	3^{ab}	1^{ab}	1^{b}	14^{a*}	0.0001	8^{ab}	8^{ab}	20^{b*}	45^{a*}	0.0001
Chenopodium album group$^{\gamma\tau}$	1^{τ}	1^{a}	t^{b}	1^{ab}	1^{ab}	0.7130	t^{a}	0^{b}	0^{b}	t^{ab}	0.0132
	2	1	2	12*	18*	0.0003	0*	1	t	1	0.1988
Chenopodium gigantospermum	1	1	t	t	t	0.2661	•	•	•	•	•
	2	t	•	2	2	0.1782	•	•	•	•	•
Elymus villosus	1	•	•	•	t	0.1058	•	1	t	•	0.3379
	2	•	t	•	2	0.1014	1	1	2	1	0.5774
Erechtites hieracifolia^{r}	1	•	•	•	•	•	•	•	•	•	•
	2	•	•	•	4	0.3976	•	•	•	t	0.3976
Eupatorium rugosum	1	2	8	1	3	0.0771	8^{a}	2^{b}	2^{ab}	11^{ab}	0.0123
	2	1	11	6	15*	0.0559	3	1	8*	22	0.0001
Festuca obtusa	1^{τ}	t	t	t	•	0.7615	2^{a}	2^{ab}	0^{b}	6^{ab}	0.3167
	2	•	•	•	•	•	13	3	•	13	0.0389
Galium aparine	1^{τ}	•	t	t	t	0.6547	1^{b}	t^{b}	3^{b}	1^{a}	0.2658
	2	t	t	t	2	0.0297	1	2	7*	9*	0.0029
Hackelia virginiana	1	t	•	t	t	0.5736	•	t	•	t	0.1511
	2	0^{b}	t^{b}	7^{a*}	7^{a*}	0.0012	0^{b}	t^{b}	3^{a*}	6^{a*}	0.0001
Teucrium canadense	1	0^{b}	8^{a}	0^{b}	t^{b}	0.0011	0^{b}	2^{a}	0^{b}	0^{b}	0.0404
	2	0^{b}	13^{a*}	0^{b}	2^{b}	0.0001	0^{b}	2^{a}	t^{b}	t^{b}	0.0606
Urtica dioica	1^{τ}	0^{b}	5^{a}	0^{b}	1^{b}	0.0043	•	1	•	•	0.3976
	2	0^{b}	11^{a}	0^{b}	1^{b}	0.0004	t^{b}	1^{a}	0^{b}	t^{b}	0.5028

Notes: Species listed include *Q. macrocarpa* and all species with an average canopy of 5% or more in either year for any treatment. *F*-value is from nonparametric one-way ANOVA among treatment plots at a site. Nomenclature follows the Great Plains Flora Association (1986). Dots (•) are used in place of zero cover values for visual clarity.

\# = Part of the burn-thin plot and all of the burn-clear plot were not burned.

τ = Significant difference in understory canopy cover between study sites where all treatment plots at a site were combined ($p \leq 0.05$; nonparametric one-way ANOVA).

γ = *Parthenocissus* spp. includes at least *Parthenocissus quinquefolia*, and *Symphoricarpos* spp. includes at least *Symphoricarpos orbiculatus*.

* = Significant difference between Years 1 and 2 for species indicated (Student's t-test).

a, b, c = Different alphabetic superscripts indicate statistically significant differences ($p \leq 0.05$) among treatment plots as determined by the Student-Newman-Keuls multiple comparison test. Values with the same superscript or without alphabetic superscripts among treatments for any year did not differ significantly.

‡ = Species considered to be invasive or non-native (Great Plains Flora Association 1986).

t = trace (<1% cover value).

r = Species considered to be ruderal (Great Plains Flora Association 1986).

TABLE 2
PERCENTAGE OF UNDERSTORY COVER AT HITCHCOCK NATURE CENTER STUDY SITES BY TREATMENTS FOR YEAR 1 (PRE-TREATMENT) AND YEAR 2 (POST-TREATMENT)

		Site 1					Site 2				
Cover groups	**Year**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	***F*-value**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	***F*-value**
Total cover	1	79	88	89	82	0.0461	80^{bc*}	94^{a}	88^{ab}	76^{c}	0.0009
	2	30*	16*	25*	53*	0.0001	43^{b*}	51^{b*}	71^{a*}	80^{a}	0.0001
Woody species	1	3^{b}	2^{b}	3^{a}	14^{a}	0.0044	6^{ab}	5^{ab}	6^{b}	18^{a}	0.0110
	2	18*	15*	6	10	0.0034	12^{b}	21^{ab*}	23^{ab*}	35^{a*}	0.0007
Graminoid	1^{τ}	2	t	1	1	0.2838	5^{a}	1^{b}	1^{ab}	4^{a}	0.0324
	2	6^{b}	1^{b}	4^{b*}	15^{a*}	0.0008	15^{a*}	3^{b*}	13^{a*}	48^{a*}	0.0001
Forbs	1^{τ}	2^{a}	t^{b}	2^{b}	3^{b}	0.4597	4^{ab}	12^{a}	5^{b}	5^{ab}	0.0038
	2	3^{b}	2^{b}	12^{a*}	34^{a*}	0.0001	12*	26	47*	43*	0.0001
Bare soil	1^{τ}	20	15	12	11	0.6261	29	19	38	31	0.1803
	2	10	14	22	40*	0.0008	18^{b}	26^{a}	45^{a}	29^{a}	0.0182
Litter	1^{τ}	81	82	88	89	0.5940	72	72	62	70	0.5351
	2	81^{a}	76^{a}	59^{ab*}	42^{b*}	0.0001	65^{a}	60^{a}	39^{b*}	59^{a}	0.0202

		Site 1					Site 2				
Woody species	**Year**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	***F*-value**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	***F*-value**
Celtis occidentalis	1	1^{ab}	1^{ab}	2^{b}	2^{a}	0.8069	2^{a}	0^{b}	0^{b}	3^{a}	0.0513
	2	1	1	t	5	0.0009	4^{a}	2^{a*}	3^{b*}	6^{a}	0.2337
Cornus drummondii‡	1	t	•	•	•	0.1058	t	•	•	1	0.3870
	2	t	•	•	•	0.1058	•	•	•	1	0.3976
Fraxinus pennsylvanica	1	t	•	•	•	0.0614	•	•	•	t	0.3976
	2	t	•	•	t	0.4910	•	1	t	t	0.6039
Ostrya virginiana	1	2	1	2	6	0.4303	1^{c}	4^{ab}	3^{a}	2^{bc}	0.2396
	2	4	3*	1	t	0.0326	1^{bc}	2^{ab}	4^{a}	t^{c}	0.0018
Parthenocissus spp.$^{\gamma}$	1^{τ}	t	1	t	3	0.2549	3^{a}	6^{a}	1^{b}	5^{a}	0.0308
	2	2*	2	1	3	0.4383	11^{a*}	8^{a}	11^{b*}	13^{a*}	0.7687
Quercus macrocarpa	1	•	3	•	•	0.3976	t	•	•	t	0.4596
	2	•	2	•	•	0.3976	•	•	•	•	•
Ribes missouriense	1^{τ}	t	•	•	•	0.3976	t	4	•	2	0.0590
	2	t	t	t	•	0.5736	0^{b}	3^{a}	t^{b}	5^{a}	0.0189
Rubus occidentalis	1	•	•	•	•	•	•	•	•	•	•
	2	0^{b}	0^{b}	t^{b}	1^{a}	0.1195	t	•	t	•	0.2919
Symphoricarpos spp.‡$^{\gamma}$	1	3	t	•	t	0.1534	t^{ab}	1^{ab}	0^{b}	2^{a}	0.3784
	2	4^{a}	t^{ab}	0^{b}	2^{ab}	0.1001	t^{b}	t^{b}	t^{b}	5^{a}	0.0029

Table 2 continued

Herbaceous species	Year	Site 1 Control	Site 1 Burn-only	Site 1 Burn-thin	Site 1 Burn-clear	Site 1 *F*-value	Site 2 Control	Site 2 Burn-only	Site 2 Burn-thin	Site 2 Burn-clear	Site 2 *F*-value
Carex spp.	1	1	t	1	2	0.1012	2^{a}	t^{bc}	1^{ab}	t^{c}	0.0044
	2	3^{b}	1^{b}	4^{b*}	10^{a}	0.0221	12^{a*}	1^{b*}	11^{a*}	10^{b*}	0.0368
Chenopodium album group[γr]	1	•	•	•	•	•	•	•	•	•	•
	2	0^{c}	t^{b*}	1^{ab*}	8^{a*}	0.0001	t^{b}	0^{b}	1^{ab}	1^{a*}	0.3181
Chenopodium gigantospermum	1	•	•	•	•	•	•	•	•	•	•
	2	0^{b}	t^{b}	t^{b}	6^{a*}	0.0023	t	t	•	•	0.2919
Elymus villosus	1^{τ}	t	•	t	t	0.3262	1^{b}	t^{b}	t^{b}	3^{a}	0.0160
	2	1	t	t	4	0.0883	1^{b}	1^{b}	2^{b}	33^{a*}	0.0001
Erechtites hieraciifolia[r]	1	•	•	•	•	•	•	•	•	•	•
	2	0^{b}	t^{b}	1^{a*}	t^{b}	0.0024	0^{c}	t^{c}	17^{a*}	7^{b*}	0.0001
Eupatorium rugosum	1^{τ}	1	t	t	2	0.3965	2	8	4	3	0.2155
	2	2	t	2	8	0.0068	7*	20	22*	29*	0.0264
Festuca obtusa	1	•	•	•	•	•	•	•	•	•	•
	2	•	•	•	•	•	1^{a}	t^{b}	0^{b}	5^{a*}	0.0195
Galium aparine	1	•	•	•	•	•	•	•	•	•	•
	2	•	•	•	t	0.3976	•	•	•	1	0.3976
Hackelia virginiana	1	t	•	•	•	0.2455	t	t	•	t	0.5641
	2	t	t	t	2	0.0375	0^{b}	0^{b}	1^{a}	0^{b}	0.0947
Teucrium canadense	1	•	•	•	•	•	•	•	•	•	•
	2	•	•	•	•	•	•	•	•	t	0.3976
Urtica dioica	1	•	•	•	•	•	•	•	•	•	•
	2	•	•	•	•	•	•	•	•	•	•

Notes: Species listed include *Q. macrocarpa* and all species with an average canopy of 5% or more in either year for any treatment. *F*-value is from nonparametric one-way ANOVA among treatment plots at a site. Nomenclature follows the Great Plains Flora Association (1986). Dots (·) are used in place of zero cover values for visual clarity.

[a, b, c] = Different alphabetic superscripts indicate statistically significant differences ($p \leq 0.05$) among treatment plots as determined by the Student-Newman-Keuls multiple comparison test. Values with the same superscript or without alphabetic superscripts among treatments for any year did not differ significantly.

* = significant difference between Years 1 and 2 for species indicated (Student's t-test).

τ = significant difference in understory canopy cover between study sites where all treatment plots at a site were combined ($p \leq 0.05$; nonparametric one-way ANOVA).

t = trace (<1% cover value).

‡ = Species considered to be invasive or non-native (Great Plains Flora Association 1986).

[γ] = *Parthenocissus* spp. includes at least *Parthenocissus quinquefolia*, and *Symphoricarpos* spp. includes at least *Symphoricarpos orbiculatus*.

r = Species considered to be ruderal (Great Plains Flora Association 1986).

TABLE 3
SHANNON DIVERSITY (H') AND SPECIES RICHNESS (S) BEFORE AND AFTER TREATMENT

	Five Ridge Prairie						Hitchcock Nature Center					
	Pre-treatment		Post-treatment				Pre-treatment		Post-treatment			
Treatment	**H'**	**S**	**H'**	**S**	**t**	***p***	**H'**	**S**	**H'**	**S**	**t**	***p***
Control	2.489	38	2.480	42	0.104	0.921	2.571	24	2.426	33	2.359	0.056
Burn-only	2.597	39	2.936	47	-4.969	0.003	2.072	18	2.176	28	-1.116	0.307
Burn-thin	1.720	34	2.670	49	-10.81	<0.001	1.816	14	2.493*	42	-8.709	<0.001
Burn-clear	2.310	46	2.866	56	-8.103	<0.001	2.441	24	2.728**	50	-4.127	0.006

t = critical value (Student's t-test, $p \leq 0.05$) (Zar 1999).
* = Incomplete burn
** = Unburned

Prairie) than at the southern sites (Hitchcock Nature Center) (Table 3). Averaged over both sites, the increase in Shannon diversity was least for the lowest intensity treatment (burn-only) (H' increased 8.7%), intermediate for plots burned and cleared (burn-clear) (H' increased 15.1%), and greatest for burned and thinned plots (burn-thin; H' increased 31.5%). Diversity declined 3.1% in control plots (control). Similar responses were observed for species richness (S), although the effect was more pronounced at the southern study area (Hitchcock) where all treatment plots were successfully burned. In the Hitchcock plots, the number of species increased 27.3% without treatment (control), 35.7% in burn-only plots, 66.7% in burn-thin plots, and 52% in burn-clear plots. The background changes in richness may reflect sampling at different times of year before and after treatment.

Changes in Cover and Density in the Understory

Effects on Species Groups. Among understory plant groups, forb cover was most consistent in its response to treatments, increasing significantly from an average of 8% before treatment to 41% after treatment in burn-clear plots, from 4% to 26% in burn-thin plots, and from 11% to 20% in burn-only plots, although the latter increase was significant only for Five Ridge Prairie Site 1 (Tables 1–2). Without treatment (control), overall forb cover remained at 6% before and after treatment. Graminoid cover for combined sites increased from 8% to 34% in burn-clear plots, although the increase was significant only in three of four plots. Similarly, increases in graminoid cover in burn-thin plots (from 2% to 10%) were significant in three of four burn-thin plots, although this increase was substantially less than with burning and clearing (burn-clear). By contrast, changes in understory woody species were variable. For example, at Five Ridge Prairie, woody cover declined from 53% to 33% in all six treated plots, with declines significant in all but the burn-clear plot at Site 2. Meanwhile, at Hitchcock Nature Center, average understory woody species cover increased from 8% to 18% in the six treated plots, with increases significant in four plots (Tables 1–2).

Effects on Individual Herbaceous Species. While there were generally consistent trends in species group responses, differences in individual species varied considerably among and within treatments.

Burn-Clear. The greatest average post-treatment increase in herbaceous cover among all sites was recorded for *Carex* spp. (sedge) (from 6% to 20%) and *Eupatorium rugosum* (white snakeroot) (from 5% to 19%), with both increases occurring in burn-clear plots at both study areas (Tables 1–2). Increases in *Carex* spp., which likely included *Carex blanda* and *Carex sprengelii*, were significant in all study sites, but in only two of the four sites for *Eupatorium rugosum*. *Festuca obtusa* (nodding fescue) and *Elymus villosus* (hairy wildrye) were important graminoids in the understory whose cover increased in all burn-clear plots in which they occurred (from 2% to 5% and from 1% to 10%, respectively), although increases for each species were significant only in one treatment plot at each study area.

Burn-Thin. At both study areas, the second-greatest increase in overall herbaceous cover occurred in burn-thin plots. As with the burn-clear treatment, the greatest

average increases in cover occurred for *Carex* spp. (from 1% to 9%) and *Eupatorium rugosum* (from 2% to 10%) with increases significant in two of the three treated plots (Tables 1–2). *Hackelia virginiana* (stickseed) cover also increased in burn-thin plots (on average from <1% to 3%), although the change was significant at Five Ridge Prairie. *Erechtites hieracifolia* cover increased significantly, from 0% to 9%, in the two Hitchcock Nature Center burn-thin plots but was absent from the Five Ridge Prairie burn-thin plots.

Burn-Only. The greatest change in cover for burn-only plots was a significant increase in *Teucrium canadense* (American germander) (8% to 13%) in a single plot (Five Ridge Prairie Site 1). For all other herbaceous species, only slight changes in cover were recorded, with increases in some and decreases in others (Tables 1–2).

Control. In the absence of burning and tree-cutting, the greatest average increase in the herbaceous community for all sites was recorded for *Carex* spp. at one Hitchcock Nature Center site (Site 2) where cover increased from 2% to 12% (Tables 1–2). The response of *Eupatorium rugosum*, the species with the second-highest cover, was not consistent between study areas, although it increased significantly, from 2% to 7%, at Hitchcock Nature Center Site 2.

Effects on Woody Species. Of the 31 woody understory species recorded, pre-treatment cover of five species averaged greater than 1% for all plots: *Celtis occidentalis* (14%), *Cornus drummondii* (rough-leaved dogwood) (6%), *Ostrya virginiana* (3%), *Parthenocissus* spp. (Virginia creeper) (3%), and *Fraxinus pennsylvanica* (green ash) (2%) (Tables 1–2). As with herbaceous species, the response of individual woody plant species varied between study areas and between and among treatments.

Of the five woody understory species with the highest pre-treatment cover, the most consistent response among treatments was at Hitchcock Nature Center, where *Parthenocissus* spp., a woody vine, increased, often significantly, but irrespective of treatment. Changes in cover of *Parthenocissus* spp. in the northern study area (Five Ridge Prairie), however, lacked any discernible pattern. For *Celtis occidentalis*, the understory tree species with the highest average cover, response to treatment differed between study areas. At Five Ridge Prairie, *Celtis occidentalis* average cover decreased from 30% before treatment to 14% after treatment in combined burned plots (n = 6), with the decrease significant only in burn-only and burn-thin treatments (Tables 1–2). In contrast, while substantially lower in cover in the southern site (Hitchcock Nature Center), the cover of *Celtis occidentalis* increased from 1% to 3% within treatment plots, with increases significant in 2 of the 6 plots. Inconsistent patterns in response to treatment were observed for *Cornus drummondii*, *Ostrya virginiana*, and *Fraxinus pennsylvanica*, although the differences between pre- and post-treatment were generally not significant for these species.

For *Quercus macrocarpa*, the dominant tree of historic savannas in the region, average cover increased from 1% to 2% in the two treatments that involved tree-cutting. Only in Site 2 at Five Ridge Prairie, however, did *Quercus macrocarpa* occur in more plots after burning than before (3 plots vs. 1 plot, respectively) (Tables 1–2).

Effects on Litter Cover. Bare soil increased from an average for all treated plots (n = 12) of 12% before treatment to 21% after treatment (from 3% to 13% for Five Ridge Prairie and 21% to 29% for Hitchcock Nature Center). Litter cover for the same plots decreased from an average of 85% to 66% after burning (from 93% to 76% for Five Ridge Prairie and from 77% to 56% for Hitchcock Nature Center).

Changes in Cover and Density in the Overstory

Effects on Density and Canopy Cover. As designed, the most intense treatment (burn-clear) removed all woody species ≥1 cm diameter at breast height. Less intense tree removal (burn-thin) resulted in an average reduction from 15 to 3 individuals per 100 m^2 (9 to 3 at Five Ridge Prairie and 22 to 2 at Hitchcock Nature Center) (Table 4). Based on combined treatment plots, average overstory canopy cover declined from 94% to 69% for burn-thin treatments and from 95% to 15% for burn-clear treatments (Table 5). The 15% canopy cover recorded in the burn-clear plots was a function of the wide view of the densiometer reflecting the canopy of large trees uphill from the plot. The control and burn-only plots at Hitchcock Nature Center showed no change in overstory canopy cover, but at Five Ridge Prairie, small declines from 94% to 87% cover were observed for burn-only and from 94% to 90% cover for control. These differences are within the margin of error for spherical densiometers.

Stand basal area also changed predictably in response to treatment. Average control-plot basal area remained the same from before (31.5 m^2 ha^{-1}) to after (31.4 m^2 ha^{-1}) treatment. Burn-only plots increased slightly in average basal area from 55.4 m^2 ha^{-1} to 58.4 m^2 ha^{-1}. Burn-thin plots were reduced in average basal area from 34.8 m^2 ha^{-1} before treatment to 21.0 m^2 ha^{-1} after treatment.

TABLE 4
DENSITY (NUMBER OF INDIVIDUALS PER 100 M^2) OF OVERSTORY SPECIES ≥1 CM DBH BY SPECIES, STUDY SITE, AND STUDY AREA

		Five Ridge Prairie								Hitchcock Nature Center							
		Site 1				Site 2				Site 1				Site 2			
Species	**Year**	**Control**	**Burn-only**	**Burn-thin***	**Burn-clear***	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**	**Control**	**Burn-only**	**Burn-thin**	**Burn-clear**
Celtis occidentalis	1	•	•	1	1	•	•	•	•	4	1	•	6	•	•	•	•
	2	•	3	•	•	•	•	•	•	4	1	•	•	•	•	•	•
Cornus drummondii	1	10	1	4	4	•	2	•	1	•	•	•	•	•	•	•	•
	2	21	•	•	•	•	1	•	•	•	•	•	•	•	•	•	•
Fraxinus pennsyl-vanica	1	1	•	•	•	•	•	•	•	1	2	•	1	•	2	2	•
	2	1	•	•	•	•	•	•	•	•	2	•	•	•	3	•	•
Gleditsia triacanthos	1	•	•	•	•	•	•	•	•	1	•	•	•	•	•	•	•
	2	•	•	•	•	•	•	•	•	1	•	•	•	•	•	•	•
Juniperus virginiana	1	•	•	•	•	•	•	•	•	•	•	•	1	•	•	•	•
	2	•	•	•	•	•	•	•	•	•	v	•	•	•	•	•	•
Ostrya virginiana	1	•	•	•	•	9	•	8	5	15	21	24	15	24	18	11	13
	2	•	•	•	•	8	•	•	•	12	18	•	•	25	18	•	•
Quercus macrocarpa	1	2	3	2	3	1	7	3	1	2	2	4	2	5	1	1	•
	2	2	3	2	•	1	7	4	•	2	2	3	•	5	1	•	•
Quercus rubra	1	•	•	•	•	•	•	•	•	•	•	•	2	•	•	•	•
	2	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ulmus americana	1	•	•	•	•	•	•	•	•	•	•	•	•	1	•	1	•
	2	•	•	•	•	•	•	•	•	3	•	•	•	•	•	•	•
Total	1	14	4	7	8	10	9	11	7	24	26	28	27	30	22	15	13
	2	24	6	2	•	9	8	4	•	22	23	3	•	30	23	•	•

Notes: Year 1 = pre-treatment; Year 2 = post-treatment. Dots (·) are used in place of zeros for visual clarity.
* = Part of the burn-thin plot and the entire burn-clear plot were not burned.

Burn-clear plots had an average of 27.9 m^2 ha^{-1} basal area before treatment, and an absence of woody species stems above 1.37 m following treatment.

CONCLUSIONS

In general, across treatments we observed a substantial increase in diversity with burning and tree removal. This result, at least initially, appears to be consistent with other studies on savanna restoration in the Midwest (e.g., Apfelbaum and Haney 1987). The greatest diversity in our treatments (H′ = 1.77 to 2.58) resulted from burning and thinning, which might be considered an intermediate level of disturbance between burning only and clear-cutting with burning. With burning only, the amount of light reaching the understory was likely

TABLE 5
PERCENTAGE OF OVERSTORY CANOPY COVER BY YEAR FOR EACH STUDY SITE, STUDY AREA, AND TREATMENT PLOT

		Five Ridge Prairie			Hitchcock Nature Center	
Study area	Treatment	2003	2004	2005	2003	2004
1	Burn-only	90	93	80	89	95
2	Burn-only	89	95	94	87	94
1	Burn-clear	92	95	1	96	14
2	Burn-clear	93	97	18	91	26
1	Burn-thin	90	96	44	91	72
2	Burn-thin	94	97	86	93	75
1	Control	88	91	85	93	95
2	Control	94	96	95	95	97

to have been insufficient to allow germination or growth of shade-intolerant species that could respond to the greater light levels in treatments involving tree removal (Peterson et al. 2007). With clear-cutting, full sunlight (except for shading from the forest edge) could reach more of the ground for longer periods of time than in thinned forest-canopy plots. As a result, species better adapted to respond to full sunlight may have increased their canopy cover in the second year of sampling, thereby reducing the sunlight needed by species requiring high light conditions. The intermediate level of disturbance, burning and canopy thinning, created a patchwork of light levels in the treatment units, from full sunlight to full shade. As a result, a greater range of species could potentially occupy the space (i.e., those suited to either grasslands or woodlands [Leach and Givnish 1999]). This idea is also consistent with Grime's (1973) discussion of the role that intermediate levels of disturbance play in structuring plant community diversity. For example, forest species such as *Osmorhiza longistylis* (anise root) were present in burn-thin plots but not in burn-clear plots, and sun-requiring species such as *Solanum ptycanthum* (black nightshade) were present in burn-thin plots but not in burn-only plots.

Understory Cover by Plant Groups

With but one exception (graminoids at Five Ridge Prairie Site 1, burn-thin plot), average cover of graminoids and forbs increased significantly in plots with tree-thinning or clearing. Forbs were most responsive to this treatment. Increases in cover of herbaceous groups associated with treatment intensity, particularly the greater response of forbs, appears to be a consequence of increasing light levels in the forest. Similarly, observed increases in bare soil and concurrent decreases in litter cover in burned plots may have encouraged establishment of prairie species. Herbaceous species contributing most to increased understory cover were sedges and woodland forbs, which increased in abundance when light levels increased. This may represent an early stage in the recovery of savannas after decades of fire suppression and forest succession (Peterson et al. 2007). After several years of treatment, later stages may involve colonization of plants commonly thought of as prairie species, such as *Andropogon scoparius* (little bluestem) and *Bouteloua* (grama grass) species. Importantly, increases in these groups, particularly graminoids, increased fine-fuel loads, resulting in conditions more suitable to future higher-intensity burning than presently is possible in these stands. The ability to carry fire is necessary, both in the restoration of *Quercus* savanna and in maintaining natural dynamics of the ecosystem.

Changes in understory woody species in response to treatment were more variable but consistent with results reported in other studies (e.g., Nuzzo et al. 1996). The increase in woody plant cover at Hitchcock Nature Center and decrease at Five Ridge Prairie may reflect less rainfall (approximately 18 cm per year), a shorter growing season, or other differences in the north compared to the south, as suggested by Trecek-King (2003). Other explanations for these differences, such as biotic interactions or abiotic stresses and treatment conditions, cannot be excluded. Despite the short post-treatment sampling period

evaluated in this study, possible longer-term effects are indicated. For example, the slight reduction in overstory *Ostrya virginiana* density with fire treatment alone at the southern site (Hitchcock Nature Center) may represent a significant effect because *Ostrya virginiana* is a forest understory tree. This result suggests that fire alone may affect thin-barked woody plants, which are common in forest environments. Another effect suggested in this study is that manual woody plant removal may be necessary to increase herbaceous cover, and hence fine-fuel loading, in order to support fires sufficiently intense so as to reduce woody plant cover in the understory. Whether fuel loading from sedges and forest herbs is sufficient to kill mature trees in the Loess Hills is not known, but studies from other midwestern savanna restoration efforts suggests that such effects may occur if treatments are repeated frequently (Chapman and Brewer 2008). Similarly, burning at different times of year, such as summer or fall, could also differently affect the results.

Understory Cover by Species

Herbaceous Species. As treatment intensity increased, subsequent herbaceous cover increased in several species (Tables 1–2). In particular, native and nonnative herbaceous species associated with prairies or open habitats either occurred for the first time or were greater in number where canopy cover was reduced (e.g., *Verbena stricta* [hoary verbena]), whether resulting from burning or tree removal (see complete table in McKenzie 2006). These increases included graminoids (e.g., *Festuca obtusa* and *Elymus villosus*).

Among all species, the greatest significant increase in cover was in *Carex* spp. and *Eupatorium rugosum* in burned and cleared plots and in burned and thinned plots, respectively. Several *Carex* species are common in native prairie habitat, so the increase of this genus may be consistent with an increase in prairie species with treatment intensity, but many *Carex* species are also present in regional woodlands. However, while ubiquitous in regional woodlands, *Eupatorium rugosum* is rare in native prairies, although it was probably a component of historical savanna ecosystems and is known to increase following fire (Nuzzo et al. 1996). In plots that were burned and clear-cut, *Erechtites hieracifolia*, *Hackelia virginiana*, and *Galium aparine* (stickweed bedstraw) increased significantly, while *Festuca obtusa* and *Elymus villosus*, common forest understory graminoids, increased, albeit not significantly. These changes indicate the importance of opening the canopy during the savanna restoration process.

Rapid increase in cover of some graminoids and forbs suggests a robust soil seed bank or more likely, the abundance of wind-dispersed seeds. However, the absence of some of the most common prairie species (e.g., *Andropogon scoparius* and *Bouteloua* species) after treatment suggests that natural restoration of the understory herbaceous components of savanna in the study region will likely be a lengthy process.

Woody Species (<1 cm dbh). Most understory woody species declined with treatment, although declines were not in proportion to treatment intensity, and most woody species were still present in the understory after treatment. One possible example of woody plant reduction was the significant decline in *Cornus drummondii*, a woody shrub considered to be a successional species but one commonly found in formerly open areas, even long after canopy closure (McClain and Anderson, 1990). The susceptibility of this species to burning has been variously reported (e.g., Heisler et al. 2004). Had our sites contained a greater fine-fuel load and burned more intensely, there likely would have been a more uniform reduction of *Cornus drummondii* following fire across all sites (Haney et al. 2008). Our results suggest at least a short-term reduction of this species, but long-term studies show *Cornus drummondii* to increase with burning due to resprouting (e.g., Briggs et al. 2005).

Beyond *Cornus drummondii*, trends in other woody plant species were less clear, and they persisted in the understory after treatment. The greatest changes in cover across treatments and sites occurred with *Celtis occidentalis*, although changes were not consistent in direction and amount among treatments and study areas. However, taken together with the observed infrequent occurrence of *Quercus macrocarpa* regeneration, the persistence of *Celtis occidentalis* in our study, irrespective of treatment, suggests that at least in the southern Loess Hills (where all plots were completely burned) it has the potential ultimately to dominate these woodlands as it has elsewhere (Bellah and Hulbert 1974; Abrams 1986; Phillips 2001).

The persistence of woody plants in the understory, despite declines in cover, is consistent with results from studies by Brudvig and Asbjornsen (2005) and Ansley and Castellano (2006) who suggest that in the short term, fire alone cannot effectively reduce woody species in previous savanna areas that subsequently experienced several decades of fire suppression. In our study neither *Ostrya virginiana* nor *Parthenocissus* spp. showed discernible trends in response to treatments. *Quercus macrocarpa*, a dominant species in the historical savanna, showed little response to treatment. The short time frame of this study

was probably not sufficient to detect germination and development of this species, but other studies report fire as an essential part of *Quercus macrocarpa* regeneration success (e.g., Peterson and Reich 2001).

Overstory Woody Species (dbh ≥1 cm)

Manual removal of trees in the burn-clear and burn-thin treatments greatly reduced the density of tree species with a diameter at breast height ≥1 cm. These effects appeared to be exclusively the result of manual tree removal. We saw only slight declines in density (from 21 to 18 individuals/100 m^2) of *Ostrya virginiana* at the southern study area (Hitchcock Nature Center), although this may reflect sampling error rather than an actual decline in cover. This result, however, is consistent with results reported by Brown (1960) even though the duration of our study was too short term to definitely identify a pattern of decline. Daubenmire (1936) also observed that after long fire-free intervals, fire decreased *Ostrya virginiana* populations in the Minnesota "Big Woods." However, top-killed *Ostrya virginiana* trees have been observed to resprout (Swan 1970), suggesting the need for repeated burning if complete removal of resprouting species is a management objective. In the burn-thin plots we removed all species except *Quercus macrocarpa*, and in the burn-clear plots, we removed all woody species. It is important to note that different tree species can affect aspects of community structure and function in different ways, and the removal of one species may have more substantial and immediate effects on the community as compared to the removal of another species (Ellison et al. 2005).

Our results suggest that in the short term, a combination of burning and tree-cutting has the potential to increase the cover and diversity of herbaceous species in former Loess Hills savanna communities, although many of these may be either ruderal or woodland species. An increase in graminoids is particularly important because it reflects an increase in the amount of fine fuel, which can increase fire intensity and the concomitant mortality of woody plants (Fuhlendorf and Smeins 1997). Removal of more tree canopy can result in greater amounts of fine fuel in the understory, and species diversity may be greatest when some trees remain, probably due to variable light levels, allowing a mixture of shade-tolerant and shade-intolerant species to coexist. A single burn, however, does not appear to effectively reduce tree canopy, even though fire has been shown to be important for maintaining established savanna (e.g., White 1983; Peterson and Reich 2001). A single burn, however, does appear to increase fine-fuel loads for future burns. Overall, our results suggest that restoration of savanna understory species in the Loess Hills can be initiated with tree-cutting and fire. Restoration of an oak savanna with prairie plants in the understory, however, will most likely require repeated treatments to control undesirable woody plants, and to provide conditions for a sufficient period of time for prairie or savanna species to become established.

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REFERENCES

Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29–37.

Abrams, M.D. 2003. Where has all the white oak gone? *Bioscience* 53:927–39.

Aikman, J.M., and A.W. Smelser. 1938. The structure and environment of forest communities in central Iowa. *Ecology* 19:141–50.

Anderson, R.C. 1991. Savanna concepts revisited. *BioScience* 41:371.

Anderson, R.C. 1998. Overview of Midwestern oak savanna. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86:1–18.

Ansley, R.J., and M.J. Castellano. 2006. Strategies for savanna restoration in the southern Great Plains: Effects of fire and herbicides. *Restoration Ecology* 14:420–28.

Apfelbaum, S.L., and A. Haney. 1987. Management of degraded oak savanna remnants in the Upper Midwest: Preliminary results from three years of study. In *Proceedings of the Oak Woods Management Workshop,* eds. G. Burger, J. Ebinger, and G. Wilhelm. Eastern Illinois University, Peoria, IL.

Bellah, R.G., and L.C. Hulbert. 1974. Forest succession on the Republican River floodplain in Clay County, Kansas. *Southwestern Naturalist* 19:155–65.

Bettis, E.A. III, J.C. Prior, G.R. Hallberg, and R.L. Handy. 1986. Geology of the Loess Hills region. *Proceedings of the Iowa Academy of Science* 93:78–85.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* 29:19–24.

Branham, C.E. 1989. *Soil Survey of Pottawattamie County, Iowa*. U.S. Department of Agriculture, Soil Conservation Service. U.S. Government Printing Office, Washington, DC.

Bray, J.R. 1960. The composition of savanna vegetation in Wisconsin. *Ecology* 41:721–32.

Briggs, J.M., A.K. Knapp, J.M. Blair, J.L. Heisler, G.A. Hoch, M.S. Lett, and J.K. McCarron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243–54.

Brown, J.H. Jr. 1960. The role of fire in altering the species composition of forests in Rhode Island. *Ecology* 41:310–16.

Brudvig, L.A., and H. Asbjornsen. 2005. Oak regeneration before and after initial restoration efforts in a tallgrass oak savanna. *American Midland Naturalist* 153:180–86.

Chapman, K.A., and R. Brewer. 2008. Prairie and savanna in southern lower Michigan: history, classification, ecology. *Michigan Botanist* 47:1–48.

Curtis, J.T. 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press, Madison.

Daubenmire, R. 1936. The "Big Woods" of Minnesota: Its structure and relation to climate, fire, and soils. *Ecological Monographs* 6:233–68.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.

Dillon, K.R., S.H. Emerman, and P.K. Wilcox. 2006. (*Artists' Depictions of Catsteps in the Loess Hills of Iowa: Evidence for Mid-Nineteenth-Century Climate Change*). Pgs. 25–36. "Hydrology Days," Colorado State University, Fort Collins, CO.

Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–86.

Fuhlendorf, S.D., and F.E. Smeins. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science* 8:819–28.

Great Plains Flora Association. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–47.

Grundel, R., and N.B. Pavlovic. 2008. Using conservation value to assess land restoration and management alternatives across a degraded oak savanna landscape. *Journal of Applied Ecology* 45:315–24.

Haney, A., M. Bowles, S. Apfelbaum, E. Lain, and T. Post. 2008. Gradient analysis of an eastern sand savanna's woody vegetation, and its long-term responses to restored fire processes. *Forest Ecology and Management* 256:1560–71.

Heisler, J.L., J.M. Briggs, A.K. Knapp, J.M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85:2245–57.

Iffrig, G.F. 1983. Distribution and ecology of Loess Hill prairies in Atchison and Holt Counties in northwestern Missouri. In *Proceedings of the Seventh North American Prairie Conference of 1980*, ed. C. Kucera, 129–33. Southwest Missouri State University, Springfield, MO.

Leach, M.K., and T.J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecological Monographs* 69:353–74.

Loomis, W.E., and A.L. McComb. 1944. Recent advances of the forest in Iowa. *Proceedings of the Iowa Academy of Science* 51:217–24.

McCarty, K. 1998. Landscape-scale restoration in Missouri savannas and woodlands. *Restoration and Management Notes* 16:22–32.

McClain, W.E., and E.A. Anderson. 1990. Loss of hill prairie through woody plant invasion at Pere Marquette State Park, Jersey County Illinois. *Natural Areas Journal* 10:69–75.

McKenzie, D.A. 2006. Restoration of *Quercus macrocarpa* (bur oak) savanna in Iowa's Loess Hills. Master's thesis, University of Nebraska at Omaha, Omaha, NE.

Meisel, J., N. Trushenski, and E. Weiher. 2002. A gradient analysis of oak savanna community composition in western Wisconsin. *Journal of the Torrey Botanical Society* 129:115–24.

Minitab, Inc. 2003. Minitab for Windows, Release 14. State College, PA.

MRCC (Midwest Regional Climate Center). 2009. *Historic Climate Data (1971–2000) for Le Mars, IA, and Oakland, IA*. http://mrcc.sws.uiuc.edu/climate_midwest/

mwclimate_data_summaries.htm# (accessed March 31, 2009).

Mutel, C.F. 1989. *Fragile Giants: A Natural History of the Loess Hills.* University of Iowa Press, Iowa City.

Novacek, J.M., D.M. Roosa, and W.P. Pusateri. 1985. The vegetation of the Loess Hills landform along the Missouri River. *Proceedings of the Iowa Academy of Science* 92:199–212.

Nuzzo, V.A. 1986. Extent and status of Midwest oak savanna: Presettlement and 1985. *Natural Areas Journal* 6:6–36.

Nuzzo, V.A., W. McClain, and T. Strole. 1996. Fire impact on ground-layer flora in a sand forest, 1990–1994. *American Midland Naturalist* 136:207–21.

Olson, D.F. Jr. 1974. *Quercus* L. Oak. In *Seeds of Woody Plants in the United States*, tech. coord. C.S. Schopmeyer, 692–703. Agriculture Handbook 450. U.S. Department of Agriculture, Washington, DC.

Packard, S. 1993. Restoring oak ecosystems. *Restoration and Management Notes* 11:5–17.

Perala, D.A. 1974. *Growth and Survival of Northern Hardwood Sprouts after Burning.* USDA Forest Service Research Note NC-176. North Central Forest Experiment Station, St. Paul, MN.

Peterson, D.W., and P.B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. *Ecological Applications* 11:914–27.

Peterson, D.W., P.B. Reich, and K.J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science* 18:3–12.

Phillips, P. 2001. Age structure, species composition and succession in a Loess Hills woodland. Master's thesis, University of Nebraska at Omaha, Omaha, NE.

Rebertus, A.J., and B.R. Burns. 1997. The importance of gap processes in the development and maintenance of oak savannas and dry forests. *Journal of Ecology* 85:635–45.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Wiens. 1981. *The True Prairie Ecosystem.* United States/International Biological Program Synthesis Series, vol. 16. Hutchinson Ross Publishing Company, Stroudsburg, PA.

Roosa, D.M., D.R. Farrar, and M. Ackelson. 1986. Preserving natural diversity in Iowa's Loess Hills: Challenges and opportunities. *Proceedings of the Iowa Academy of Science* 93:163–65.

Rosburg, T.R., and D.C. Glenn-Lewin. 1996. Species composition and environmental characteristics of grassland and ecotonal plant communities in the Loess Hills of western Iowa (USA). *Natural Areas Journal* 16:318–34.

Royce, J., M.A. Arthur, A. Schörgendorfer, and D.L. Loftis. 2010. Establishment and growth of oak (*Quercus alba, Quercus prinus*) seedlings in burned and fire-excluded upland forests on the Cumberland Plateau. *Forest Ecology and Management* 260:502–10.

Russell, F.L., and N.L. Fowler. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. *Southwest Naturalist* 44:31–41.

SAS Institute, Inc. 1999. SAS System for Windows Version 8. Cary, NC.

Stambaugh, M.C., R.P. Guyette, and E.R. McMurry. 2006. Fire history at the eastern Great Plains margin, Missouri River Loess Hills. *Great Plains Research* 16:149–59.

Swan, F.R. Jr. 1970. Post-fire response of four plant communities in south-central New York state. *Ecology* 51:1074–82.

Tinus, R.W. 1980. *Raising Bur Oak in Containers in Greenhouses.* U.S. Department of Agriculture, Forest Service, Research Note RM-384. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Trecek-King, M. 2003. Woody plant communities of the Iowa Loess Hills: Expansion from 1855–2000, extant composition and ecological succession. Master's thesis, University of Nebraska at Omaha, Omaha, NE.

White, A.S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. *Ecology* 64:1081–85.

Worster, J.R., and E.H. Harvey. 1976. *Soil Survey of Plymouth County, Iowa.* U.S. Department of Agriculture, Soil Conservation Service. U.S. Government Printing Office, Washington DC.

Zar, J.H. 1999. *Biostatistical Analysis*, 4th ed. Prentice-Hall, Upper Saddle River, NJ.