Evaluation of Central North American Prairie Management Based on Species Diversity, Life Form, and Individual Species Metrics

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Abstract: *Reintroduction of fire and grazing, alone or in combination, has increasingly been recognized as central to the restoration of North American mixed-grass and tallgrass prairies. Although ecological studies of these systems are abundant, they have generally been observational, or if experimental, have focused on plant species diversity. Species diversity measures alone are not sufficient to inform management, which often has goals associated with life-form groups and individual species. We examined the effects of prescribed fire, light cattle grazing, and a combination of fire and grazing on three vegetation components: species diversity, groups of species categorized by life-form, and individual species. We evaluated how successful these three treatments were in achieving specific management goals for prairies in the Iowa Loess Hills (U.S.A.). The grazing treatment promoted the greatest overall species richness, whereas grazing and burning and grazing treatments resulted in the lowest cover by woody species. Burning alone best achieved the management goals of increasing the cover and diversity of native species and reducing exotic forb and (predominantly exotic) cool-season grass cover. Species-specific responses to treatments appeared idiosyncratic (i.e., within each treatment there existed a set of species attaining their highest frequency) and nearly half of uncommon species were present in only one treatment. Because all management goals were not achieved by any one treatment, we conclude that management in this region may need refining. We suggest that a mosaic of burning and grazing (alone and in combination) may provide the greatest landscape-level species richness; however, this strategy would also likely promote the persistence of exotic species. Our results support the need to consider multiple measures, including species-specific responses, when planning and evaluating management.*

Keywords: floristic quality, grazing, habitat restoration, plant life-form groups, prairie management, prescribed fire, species diversity

Evaluación del Manejo de Praderas en Norteamérica Central con Base en la Diversidad de Especies, Formas de Vida y Medidas de Especies Individuales

Resumen: *Cada vez se reconoce que la reintroducción de fuego y pastoreo, solos o en combinación, es central para la restauración de praderas de pastos mixtos en Norteamérica. Aunque abundan los estudios ecológicos de estos sistemas, generalmente han sido de observación, o si experimentales, se han enfocado en la diversidad de especies de plantas. La medida de la diversidad de especies por si sola no es suficiente para informar al manejo, que a menudo tiene metas asociadas con los grupos de formas de vida y con especies individuales. Examinamos los efectos del fuego prescrito, de pastoreo ligero y una combinación de fuego y pastoreo sobre tres componentes de la vegetación: diversidad de especies, grupos de especies clasificadas por forma de vida y especies individuales. Evaluamos el éxito de estos tres tratamientos en el cumplimiento de metas específicas de manejo en praderas en Iowa Loess Hills (E.UA.). El tratamiento de pastoreo promovió la mayor riqueza total de especies, mientras que los tratamientos de pastoreo y*

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fuego-pastoreo resultaron en la menor cobertura de especies leñosas. El tratamiento con fuego solo permitió el mejor cumplimiento de los objetivos de manejo consistentes en incrementar la cobertura y diversidad de especies nativas y en reducir la cobertura de hierbas exóticas y pastos (predominantemente exóticos) durante la época fresca. Las respuestas de especies individuales a los tratamientos aparentemente fueron idiosincrásicas (i. e., dentro de cada tratamiento existía un conjunto de especies que alcanzaron su máxima frecuencia) y casi la mitad de las especies no comunes estuvieron presentes en solo un tratamiento. Debido a que no se cumplieron todas las metas de manejo con un tratamiento, concluimos que el manejo de esta región puede requerir refinamiento. Sugerimos que un mosaico de fuego y pastoreo (solos y combinados) puede proporcionar la mayor riqueza de especies a nivel de paisaje; sin embargo, es probable que esta estrategia también promoviera la persistencia de especies exóticas. Nuestros resultados soportan la necesidad de considerar medidas múltiples, incluyendo las respuestas de especies individuales, al planificar y evaluar el manejo.

Palabras Clave: calidad florística, diversidad de especies, fuego prescrito, grupos de formas de vida de plantas, manejo de praderas, pastoreo, restauración de hábitat

Introduction

Fire and grazing by a diverse group of native herbivores were historically important processes that shaped the North America prairies (Axelrod 1985). Nevertheless, following Euro–American settlement, the landscape was highly altered by agricultural practices, habitat fragmentation, fire cessation, and the extirpation of most native large-bodied herbivores (Whitney 1994). In attempts to restore ecosystem integrity, land managers have reintroduced grazing and prescribed fire to many prairie remnants. Ecological studies of the effects of these management practices have been conducted for a number of years (reviewed in Knapp et al. 1998). Early work tended to have low levels of replication or to be observational. Some early studies used yield or biomass as the response variable, making comparisons with later studies based on plant abundance difficult (e.g., Drew 1947; Kucera & Ehrenreich 1962; Ehrenreich & Aikman 1963). More recent experimental work has focused principally on plant species diversity (e.g., Collins 1987; Howe 1994; Hartnett et al. 1996), which reflects broader concerns with conservation of biodiversity (Bestelmeyer et al. 2003).

Although there is evidence that plant diversity influences a variety of ecosystem processes in prairie systems (e.g., Tilman & Downing 1994; Tilman et al. 2001; Wilsey & Polley 2002), studies focused solely on diversity indexes provide only a partial basis for evaluation of management efforts. Because commonly used diversity indexes measure only the number of species and their relative abundances (Magurran 2004), they do not address species-specific responses to management, including those species targeted by conservationists. Indexes also mask the relative contributions of native and exotic species, whereas management generally seeks to increase the abundance of native species and decrease the abundance of exotic species (Debinski & Humphrey 1997). Results of recent work have also shown that particular species play key roles in maintaining grassland ecosystem processes. For example, legumes play a critical role in promoting experimental grassland plot productivity (Tilman et al. 1997), and warm-season grasses are functionally important for preventing invasion by exotic species in Kansas prairies (Smith et al. 2004). These results suggest that management may need to target particular species to maintain ecosystem function. Moreover, restoration efforts tend to focus on conservative species (i.e., those found only in high-quality native habitats [Swink & Wilhelm 1994]).

We assessed the impacts of three management strategies on the vegetation of Broken Kettle Grassland, a mixed-grass and tallgrass prairie in northwestern Iowa (U.S.A.). These strategies, replicated at the landscape scale, included prescribed burning, light cattle grazing, and a combination of burning and grazing treatments. To evaluate these strategies we considered the following management goals, which both broadly apply to the tallgrass prairie region and are consistent with this site's general management objectives (S. Moats, personal communication): (1) increase overall species diversity, (2) increase cover and diversity of native species, (3) decrease cover of woody, exotic forb, and exotic cool-season grass species, and (4) promote conservative and uncommon native species. To address these goals we determined the impacts of these management practices on species diversity with methods similar to those used by Collins (1987), Hartnett et al. (1996), and Collins et al. (1998). We then considered the consequences of management for several species groups (e.g., cool vs. warm-season grasses, generalist vs. conservative species). Finally, we examined species-specific responses to the treatments. Through this approach we were able to determine how effectively burning and grazing management strategies address multiple and possibly conflicting management objectives.

Methods

Study Area

We conducted this study at Broken Kettle Grassland Preserve and large tracts of private lands nearby (hereafter BKG). The BKG is a 1200-ha mixed-grass and tallgrass prairie located in Plymouth County, Iowa (42°N, 96°W), owned and managed by The Nature Conservancy (TNC) since 1991. With the inclusion of private lands under easement to TNC, the study area comprised approximately 1800 ha of prairie. Fire throughout the study area's region was largely suppressed after wide-scale Euro–American settlement began in the 1840s (Bonney 1986; Mutel 1989) and was only reestablished in the study area in 1996. Detailed land-use records are not available; however, these grasslands were likely grazed continuously for at least 100 years prior to TNC acquisition (S. Moats, personal communication).

The BKG is in the far northwestern corner of the Loess Hills, a landform of unusually thick loess deposits (20–60 m) that rises abruptly on the eastern boundary of the Missouri River floodplain and gradually decreases in height eastward. In Iowa the Loess Hills extend from north to south in a band ranging in width from 8 to 32 km. Since deposition 31,000–12,000 years ago, erosion and slumping of the fine-grained soils have resulted in a mosaic of steep ridges alternating with deep ravines. Average annual precipitation is 61 cm and average annual temperature is 9° C. Dry conditions exist during the growing season, particularly on the southwestern slopes, because of the fine, well-drained soils, intense afternoon sun, and hot, dry westerly winds (Salisbury & Dilamarter 1969; Novacek et al. 1985). The relatively high proportion of remnant prairies makes the area a high priority for prairie conservation and restoration (Mutel 1989).

Management Treatments

Twenty-four treatment units, ranging in size from 8 to 158 ha, received one of three treatments: burning ($n = 6$), grazing ($n = 6$), or burning and grazing ($n = 12$). Within each grazed and burned-and-grazed unit cattle grazing was initiated in 1997 and occurred annually between early May and early October. Within each unit cattle were allowed to graze for 3–4 weeks/year and the grazing time period was rotated so that units were grazed at different times each year. To achieve a desired postgrazing vegetation height of approximately 15 cm and to accommodate the variety of unit sizes, stocking densities varied from 25 to 130 cow/calf pairs/3- to 4-week grazing period. All grazing units were fenced. Burned and burned-and-grazed units received between one and three prescribed fires between the spring of 1997 and spring 2004. Fires occurred either in the spring before vegetation commenced growth or in the fall after senescence of the majority of the vegetation. Fire timing varied by unit; however, fall and spring timing was generally rotated within units.

Hypotheses

We hypothesized that burned-and-grazed units would support the greatest overall species diversity (goal 1) because ungulate grazing modulates species diversity through reduced dominance by warm-season grasses (e.g., Howe 1994; Collins et al. 1998; Towne et al. 2005). We used diversity metrics to evaluate this. We hypothesized that the burned and burned-and-grazed treatments would promote the greatest cover and diversity of native species (goal 2) through reduced cover by warm-season grasses and exotic species and associated increases in native forb cover (Howe 1994; Collins et al. 1998). We hypothesized that burned units would have the lowest cover of woody, exotic forb, and cool-season grasses (goal 3) because fire can effectively control these groups (Howe 1994; Hartnet et al. 1996). We used the analysis of species groups to evaluate these two hypotheses. We made no formal hypotheses regarding conservative and uncommon species (goal 4); however, the species-level analysis was instrumental in determining this outcome. Although overgrazing may result in soil compaction and exposed areas of bare soil, both of which tend to favor colonization by opportunistic species (Mazer 1989; Mabry 2002), low-intensity grazing by cattle can effectively mimic the historic bison-grazing regime (Towne et al. 2005) and thus help achieve management goals. If low-intensity grazing successfully mimics the historic grazing regime, we predict an overall increase in floristic quality with grazing, resulting in a greater proportion of conservative species.

Plot Selection and Data Collection

Within each of the 24 treatment units, we established between two and six plots with 50-m radii. The number of plots depended on the size of the unit. This resulted in 14 burned, 16 grazed, and 27 burned-and-grazed plots, for a total of 57 plots. All plot centers were at least 150 m apart; no plot center in a given treatment unit was within 50 m of another treatment unit or a road, and plot centers were at least 50 m from woodland edges. Because this study was part of a larger multitaxa assessment (Walker 2005), these criteria and the unbalanced study design were necessary to satisfy all sampling requirements in the project. Within each of the study plots, we established permanently marked 0.5×0.5 m vegetation quadrats at 5, 25, and 50 m from the plot center in each of the four cardinal directions, resulting in 12 quadrats/plot. In 2004 we sampled each quadrat's vegetation in June and July. We noted presence and visually estimated percent cover of all vascular plant species in each quadrat. We considered plants with woody stems $\geq$50 cm in height to be shrubs.

Data Analysis

We calculated species diversity metrics at the quadrat level, based on cover data (Magurran 2004). We defined species richness as the number of different vascular plant species present in the June and July samples combined. We calculated Shannon–Weiner diversity, species evenness, and Simpson's dominance based on July cover data. These are commonly used diversity measures (Magurran 2004), making our results comparable to other studies and translatable to management recommendations.

To assess treatment effects beyond the diversity metrics, species were classified by basic life-form groups: warm-season grasses, cool-season grasses, native forbs, exotic forbs, and shrubs. For the July data we examined the percentage of vegetation cover comprised by each of these life-form groups and by native and exotic species. To quantify the contribution of exotic species to overall species diversity, we recalculated species diversity metrics after removing all exotic species from the data set. In addition, we assessed native forb richness because native forbs are a common target of prairie conservation efforts.

We used coefficients of conservatism to examine whether there were qualitative differences in species composition among the treatments. Recently, coefficients of conservatism have become widely used as indicators of habitat quality and restoration success (e.g., Lopez & Fennessy 2002; Mushet et al. 2002; Cohen et al. 2004), making it important to evaluate their utility and limitations (Lopez & Fennessy 2002). Our intention was to examine the utility of coefficients of conservatism in the evaluation of prairie management. Conservative species were defined as species that only occur in intact native habitat, whereas generalist species were those that persist through human disturbance or recolonize disturbed sites (Swink & Wilhelm 1994). The most conservative species were assigned a value of 10, and the least conservative (i.e., generalist) a value of zero, and exotic species were not included in these categories (Swink & Wilhem 1994). The rationale behind this scoring system is that conservative species hold affinities for areas where the presettlement ecological processes have remained intact and such species are therefore good indicators of habitat quality. This scoring system was adapted to the Iowa flora by a panel of eight expert botanists (available from http://www.public.iastate.edu/~herbarium/coeffici.html). We recognize the limitations of a subjective index that is based on a 10-category framework. For example, it is difficult to justify important differences between a subjectively assigned value of 3 and 4. Thus, we focused on species with coefficients of conservatism of 0–2 (generalist species; reclassified as category 1) and 7–10 (specialist species; category 2). If coefficients of conservatism are useful for evaluating management, treatment differences may be reflected by changes in these two categories.

We conducted our analyses at the treatment-unit level by averaging quadrat values to arrive at $n = 6$ replicates/grazed and/burned treatments and $n = 12$ for the burned-and-grazed treatment. To compare species diversity metrics, coefficients of conservatism, and life-form groups, we used one-way analysis of variance (ANOVA) with treatment as the independent variable (SAS 2002). We examined the following (mean values per treatment unit) as dependent variables: species richness; species evenness; species diversity; dominance; percent cover of shrubs, cool-season grasses, warm-season grasses, native forbs, and exotic forbs; percent native species; and percentage of species in coefficient of conservatism classes 1 and 2. To examine pairwise differences among treatments, we conducted independent linear contrasts.

Conducting research at broad scales may limit the number of treatment replicates (Oksanen 2001; Cottenie & De Meester 2003). Additionally, with exploratory studies like this, Type II errors may lead to premature abandonment of lines of inquiry that may prove insightful and lead to further questions. Thus, we adopted a significance level of $\alpha = 0.10$, without correction for multiple tests, because each of our ANOVAs addressed a unique hypothesis and our findings were not contingent upon any one hypothesis' outcome (Cabin & Mitchell 2000).

To compare community composition across treatments, we examined common and uncommon species. We compared the difference between treatments' common species (defined as those present in $\geq$5% of quadrats for one or more treatment in the July sampling period) with multiresponse permutation procedure (MRPP) in PC-ORD (McCune & Mefford 1999). The MRPP is a nonparametric test with the null hypothesis that no differences exist between predefined groups (Zimmerman et al. 1985, McCune & Grace 2002). We defined groups as the three treatments, with the July frequency of occurrence for common species as the response variable (quadrats containing species in a unit $\div$ total quadrats in unit). We used Sørensen distances as the distance measure between units because species occurrences varied widely within and among treatments and because this approach is less likely to exaggerate the influence of outliers (McCune & Grace 2002). We then examined these species for trends across treatments and life-form groups. To address the management goal of retaining uncommon species, we defined these as native species present in $<$ 5% of quadrats in the July sampling period. We examined uncommon species for trends across treatments and life-form groups.

Results

We recorded 124 species, including 81 native forbs, 14 exotic forbs, 11 warm-season native grasses, 2 cool-season native grasses, 6 cool-season exotic grasses, 5 native shrubs, 3 native and 1 exotic tree species (seedlings), and 1 pteridophyte (Table 1).

Species Diversity

Grazed units had greater species richness (7.9 species /0.25^2 quadrat) than burned and burned-and-grazed units (6.8 and 6.6, respectively; $F = 2.67_{2,21}$, $p = 0.0929$; Fig. 1). Although not statistically significant, grazed units also displayed the highest levels of species diversity and evenness and lowest dominance, whereas burned-and-grazed and burned units generally displayed similar levels of diversity across metrics (Fig. 1).

Life-Form Groups

Striking differences were evident when species were grouped into major life-form categories. Burned units were dominated by native species (>90%; Fig. 2) and displayed the greatest cover of warm-season grasses, native forbs, and shrubs (Table 2). Conversely, grazed and burned-and-grazed units had approximately 30% lower cover by native species ($F = 10.75_{2,21}$, $p = 0.0006$; Fig. 2) and, concomitantly, greater cover by exotic forbs ($F = 4.72_{2,21}$, $p = 0.0202$, Fig. 2) and cool-season grasses compared with burned units ($F = 8.54_{2,21}$, $p = 0.0019$; Fig. 2). No differences across treatments were detected based on coefficients of conservatism (Table 2).

Although grazing units displayed the greatest overall species richness, when only native species were considered species richness in burned units was greatest ($F_{2,21} = 3.05$, $p = 0.0689$). Burned units were also consistently the most diverse in native species across the remaining diversity metrics. Richness of native forb species was similar in grazed and burned units (3.15 and 2.99, respectively) and lower in burned-and-grazed units (2.18); however, this was not statistically significant ($F = 1.99_{2,21}$, $p = 0.1619$).

Species-Level Analysis

The 33 most common species differed across the three treatments (MRPP; $A \approx 0.0537$, $p \approx 0.00068$; Table 1). This result was driven by a community composition divergence of burned units (average Sørensen distance from $\approx$ 0.60) from grazed-and-burned (average distance $\approx$ 0.52) and grazed-units (average distance $\approx$ 0.54). To interpret these results, we examined species-specific trends (Table 1).

As a group, native forbs were highly variable in their response to treatments. Nevertheless, we divided forbs into two general groups, in parallel with the MRPP results. One group ($n = 7$ species) was most frequent in the burning treatment, whereas the second group ($n = 11$) was most frequent in one of the two grazing treatments. In the second group, 8 species were most frequent in grazed units, and 3 were most frequent in burned-and-grazed units.

Four of five native warm-season grass species were most frequent in burned units. Only *Sporobolus heterolepis* (Beauv.) Kunth did not follow this trend; however, this species was the least common warm-season grass across treatments. *Dichanthelium oligosanthes* (J.A. Schultes) Gould, the one native cool-season grass of sufficient abundance for analysis, was most frequent in grazed units and of similar frequency in the other two treatments.

Like native forbs, shrubs were divided by response to the burning treatment. *Cornus drummondii* C.A. Mey. and *Rhus glabra* L. increased in the burned units, whereas *Symphoricarpos* was least frequent in burned units.

Exotic species' frequencies were reduced in burned units. All exotic forb species (*Euphorbia esula* L., *Melilotis alba* [L.] Lam., and *Melilotis officinalus* [L.] Lam.) and exotic cool-season grass species were least frequent in burned units. Similarly, the two most common exotic cool-season grasses, *Bromus inermis inermis* Leyss. and *Poa Pratensis* L., were approximately 20% less frequent in burned units compared with grazed units.

The 58 uncommon native species comprised 47 forbs, 4 warm-season grasses, 2 cool-season grasses, and 5 shrubs (Table 1). Of these, 24 (including 20 forbs) were unique to one of the three treatments. Nine species were unique to burned, 5 to burned-and-grazed, and 10 to grazed units.

Discussion

Reintroduction of fire and grazing is increasingly recognized as central to the restoration of mixed-grass and tallgrass prairies of North America (Howe 1994; Collins et al. 1998). Typically, the results of these management practices are evaluated with a variety of diversity metrics and/or by changes in abundance of life-form groups. We evaluated species diversity, life-form groups, and species-specific responses to management in an effort to address region-wide prairie restoration goals. Our results suggest that, in general, each goal can be individually addressed by one or more of the three management treatments; however, all goals are not addressed by any one treatment (Table 3). Moreover, the goals themselves could not have been framed by reference to a single metric, and the results would not have been clear had any single approach been used. Thus, we argue that insights into effective management for conservation hinge on evaluating multiple metrics, including species-specific responses, and weighing potentially conflicting outcomes.

Traditional diversity indexes would have effectively addressed only the goal of increasing overall species diversity (goal 1; Table 3) and would have indicated the exclusive use of grazing as the best management tool. Analyses

Table 1. Mean percent frequency of occurrence for common species (occurring in ≥ 5% of quadrats [total $n = 684$] for one or more treatments during the July sampling period) and number of occurrences of uncommon species (occurring in < 5% of quadrats) in a study of grazing and burning management treatments in a tallgrass prairie in western Iowa.

Species	*Life form*[a]	*c.c.*[b]	*Burning*	*Burning and grazing*	*Grazing*
Common species[c]					
Ambrosia psilostachya DC.	NF	2	4.3	5.1	16.3
Amorpha canescens Pursh	NF	8	7.4	6.8	2.1
Andropogon gerardii Vitman	WG	4	35.6	33.9	34.2
Andropogon scoparius Michx.	WG	6	25.2	14.0	20.5
Anemone cylindrical Gray	NF	7	8.0	3.6	10.5
Antennaria neglecta Greene	NF	2	5.5	0.6	3.2
Asclepias verticillata L.	NF	0	5.5	1.2	4.7
Aster ericoides L.	NF	3	22.1	19.4	14.7
Aster oblongifolius Nutt.	NF	10	4.3	5.7	1.6
Aster sericeus Vent.	NF	10	6.8	5.4	16.3
Bouteloua curtipendula (Michx.) Torr.	WG	6	50.9	32.1	28.4
Bromus inermis inermis Leyss.	ECG	NA	2.5	22.0	30.5
Comandra umbellate (L.) Nutt.	NF	6	9.8	3.3	0.1
Cornus drummondii C.A. Mey.	S	6	6.8	2.4	0.1
Dalea purpurea Vent.	NF	8	5.5	3.9	7.9
Dichanthelium oligosanthes (J.A. Schultes) Gould *var. screbnerianum* (Nash) Gould	NCG	5	4.9	4.2	10.5
Echinacea pallida (Nutt.) Nutt.	NF	7	4.3	6.3	5.3
Euphorbia esula L.	EF	NA	0.1	10.7	8.4
Galium boreale L.	NF	7	7.4	0.0	0.0
Helianthemum canadense (L.) Michx.	NF	7	2.5	3.0	8.4
Helianthus occidentalis Riddell	NF	8	5.5	7.1	4.7
Lygodesmia juncea (Pursh) D. Don ex Hook.	NF	7	8.6	6.9	4.2
Melilotus alba (L.) Lam.	EF	NA	0.1	8.3	12.1
Melilotus officinalis (L.) Lam.	EF	NA	1.2	6.3	4.2
Mentha arvensis L.	NF	4	1.8	5.7	9.0
Poa compressa L.	ECG	NA	0.1	0.0	14.7
Poa pratensis L.	ECG	NA	10.4	39.0	29.5
Rhus glabra L.	S	0	6.8	0.1	0.0
Solidago rigida L.	NF	4	6.1	4.8	7.9
Sorghastrum nutans (L.) Nash	WG	4	14.1	5.7	5.3
Sporobolus heterolepis (Gray) Gray	WG	9	1.2	6.9	4.2
Symphoricarpos species	S	0	2.5	8.6	9.0
Verbena stricta Vent.	NF	1	3.1	3.6	11.1
Uncommon species[d]					
Acer negundo L.	S	0	1	2	0
Aristida longespica Poir.	WS	5	0	1	0
Artemisia ludoviciana Nutt.	NF	2	0	2	0
Asclepias syriaca L.	NF	0	1	0	0
Asclepias tuberose L.	NF	6	2	0	0
Asclepias viridiflora Raf.	NF	6	1	0	0
Aster lanceolatus Willd.	NF	4	3	1	0
Astragalus canadensis L.	NF	4	1	0	1
Bouteloua hirsuta Lag.	WS	7	4	0	2
Brickellia eupatorioides (L.) Shinners	NF	5	1	7	6
Castilleja sessiliflora Pursh	NF	10	1	0	1
Ceanothus americanus L.	S	8	1	1	0
Cirsium flodmanii (Rydb.) Arthur	NF	6	1	4	5
Dalea candida Michx. ex Willd.	NF	10	3	5	2
Dalea enneandra Nutt.	NF	10	2	1	0
Equisetum laevigatum A. Braum	NF	5	7	9	6
Erigeron strigosus Muhl. ex Willd.	NF	2	0	1	8
Euphorbia marginata Pursh	NF	0	1	5	9
Fragaria virginiana Duchesne	NF	3	0	1	0
Grindelia squarrosa (Pursh) Dunal	NF	0	0	0	2
Gaura coccinea Nutt. ex Pursh	NF	7	0	0	1
Haplopappus spinulosus (Pursh) DC.	NF	8	0	0	1

continued

Table 1. Continued

Species	*Life form*[a]	*c.c.*[b]	*Burning*	*Burning and grazing*	*Grazing*
Juniperus virginiana L.	S	1	1	0	1
Koeleria macrantha (Ledeb.) J.A. Schultes	CG	7	2	6	1
Lactuca canadensis L.	NF	1	6	2	0
Lactuca tatarica (L.) C.A. Mey.	NF	2	3	0	2
Laportea canadensis (L.) Weddell	NF	3	1	0	0
Liatris aspera Michx.	NF	8	0	5	0
Liatris punctata Hook.	NF	8	0	2	3
Linum sulcatum Riddell	NF	7	1	9	0
Lithospermum canescens (Michx.) Lehm	NF	7	1	0	0
Mirabilis nyctaginea (Michx.) MacM.	NF	0	1	0	0
Monarda fistulosa L.	NF	0	0	2	3
Onosmodium molle Michx.	NF	4	2	0	3
Oxalis stricta L.	NF	0	1	0	2
Paspalum setaceum Michx. var. *ciliatifolium* (Michx.) Vasey	WS	4	0	0	4
Pediomelum esculentum (Pursh) Rydb.	NF	8	0	1	1
Phlox pilosa L.	NF	7	1	0	0
Physalis heterophylla Nees	NF	2	1	1	0
Physalis subglabrata Mackenzie & Bush	NF	4	0	0	5
Physalis virginiana P. Mill.	NF	4	1	2	2
Polygonatum biflorum (Walt.) Ell.	NF	4	1	0	0
Potentilla arguta Pursh	NF	8	0	0	1
Pulsatilla patens (L.) P. Mill.	NF	8	5	0	2
Ratibida columnifera (Nutt.) Woot. & Standl.	NF	4	0	0	3
Rosa arkansana Porter	S	4	7	6	2
Senecio plattensis (Nutt.) W.A. Weber & A. Löve	NF	4	3	1	5
Sisyrinchium campestre Bickn.	NF	4	1	3	2
Solidago altissima L.	NF	0	8	7	6
Solidago nemoralis Ait.	NF	4	7	2	3
Solidago speciosa Nutt.	NF	7	0	0	2
Sporobolus asper (Beauv.) Kunth	WS	3	0	0	4
Stipa spartea Trin.	CG	6	0	4	4
Ulmus americana L.	S	2	4	1	4
Urtica dioica L.	NF	0	1	1	0
Viola pedatifida G. Don	NF	8	4	2	2
Viola pratincola Greene	NF	0	0	1	0
Yucca glauca Nutt.	NF	10	1	0	0

[a] *Life-form groups: native forbs (NF), exotic forbs (EF), warm-season grasses (WG), native cool-season grasses (NCG), exotic cool-season grasses (ECG), and shrubs (S). All warm-season grasses and shrubs were native.*
[b] *Iowa coefficient of conservatism (c.c.) denotes species dependence on unaltered habitat and ranges from 0 (least dependent) to 10 (most dependent) (NA, exotic species, no coefficient assigned).*
[c] *Treatments differ in composition of common species (multiresponse permutation procedure,* $A \approx 0.054$, $p \leq 0.001$*).*
[d] *To balance unequal sample sizes, 12 plots/treatment were randomly selected for analysis of uncommon species (quadrat* $n = 168$*/treatment).*

by species groups, however, suggested that fire effectively promoted native species and reduced the abundance of shrubs, exotic forbs, and grasses (goals 2 & 3; Table 3). Finally, the species-specific analyses showed the importance of a mixture of fire, grazing, and the combination of the two because each treatment was associated with different subsets of common and uncommon species and with conservative species (goal 4; Table 3).

Our diversity results differed from past work, which reported that burning combined with grazing promotes the greatest plant diversity (Collins 1987; Howe 1994; Collins et al. 1998; Towne et al. 2005). Such variability in grassland community response to burning and grazing may be a function of differences in geographic region, climate, topography, initial species composition, and the timing and type of management (Bazzaz & Parrish 1982). Nevertheless, our results do support the contention that management recommendations based largely on diversity metrics may be erroneous (Drew 1947; Kucera 1956; Gibson et al. 1993). In addition, although burning was associated with increased dominance by warm-season grasses in our study (Collins 1987; Howe 1994; Collins et al. 1998; Towne et al. 2005), we did not find an associated decrease in native forb richness (Collins et al. 1998). In fact, burning units had the greatest richness of native forbs (and native species in general). Although the increase in warm-season grass cover was relatively modest, the decrease in exotic species in the burning units was pronounced, suggesting that this might be the mechanism promoting native diversity in this treatment.

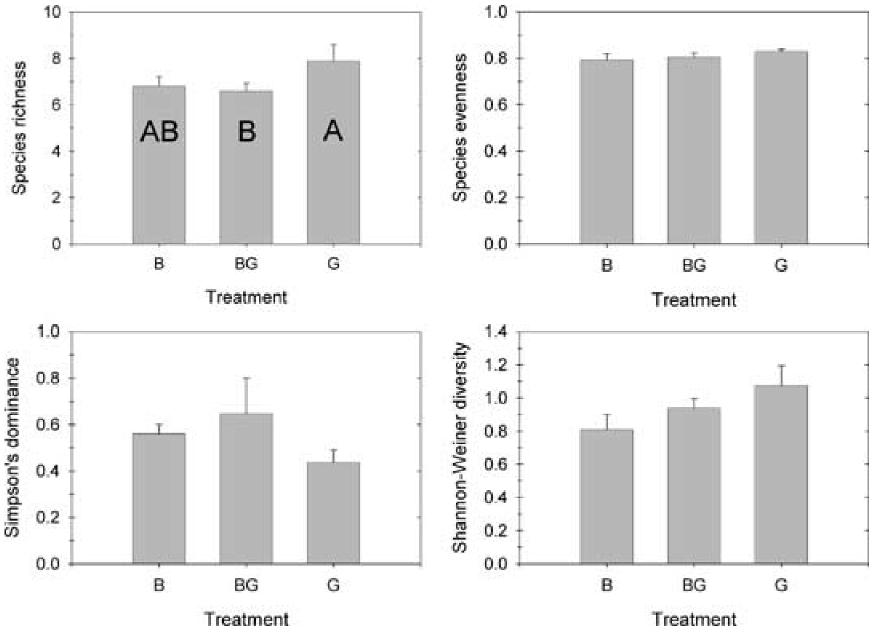

Figure 1. Species richness, evenness, Simpson's dominance, and Shannon–Weiner diversity in 0.25-m² quadrats in a study of prairie management in western Iowa. Treatments were prescribed burning (B), burning with cattle grazing (BG), and cattle grazing (G). Bars represent means + 1 SE. Different letters on bars represent significant differences between treatments (independent linear contrast following analysis of variance, α < 0.1).

Grouping species into broad categories such as cool-season grasses, exotic forbs, and native forbs is also commonly used to evaluate prairie management (Howe 1995; Collins et al. 1998; Cully et al. 2003; Towne & Kemp 2003). This approach provided some insights beyond diversity metrics. When we examined only native species, the burned units were the most diverse. This insight was initially obscured when we examined overall diversity, which was highest in the grazed units. Our results parallel results of other studies that show a positive association between exotic species and grazing or mowing in Midwestern prairies (e.g., Drew 1947; Kucera 1956; Gibson et al. 1993) and elsewhere (Harrison et al. 2003; Hayes & Holl 2003) and, conversely, a reduction of exotic species with burning (Curtis & Partch 1948; Hover & Bragg 1981; Engle & Bidwell 2001; Towne & Kemp 2003; Dornbush 2004).

Nevertheless, the species-specific analyses also highlighted potential limitations of using species groups to guide management. The species-level analysis revealed groups of species that responded positively to each treatment and suggested that all three treatments were important for promoting site-level species diversity at BKG. Common species tended to fall into one of two major groups: those that responded positively to the burning treatment and those that were promoted by one of the grazing treatments. Conversely, the response of uncommon species (predominantly forbs) was highly variable, with many found only in one treatment type. The idiosyncratic or species-specific response of forbs to management has been noted elsewhere (Curtis & Partch 1948; Dornbush 2004). Moreover, the knowledge that grazed and burned-and-grazed units had greater exotic forb and cool-season grass cover may not elucidate the most efficient management strategies. Our species-level analysis showed that the collective response of these groups was driven by only a few exotic species (e.g., *B. inermis*, *P. pratensis*), suggesting that eradication efforts might need to focus on these species.

We found no differences in coefficients of conservatism across treatments in this study (Table 2). Although it appears that the treatments were equally effective at

Table 2. Means ± 1 SE for floristic variables across grazing and burning management treatments in a tallgrass prairie in western Iowa.

Variable[a]	*ANOVA (df, F, p)*	*Grazed*	*Burned/Grazed*	*Burned*
Cover of warm-season grasses (%)	2/21, 3.70, 0.0419	17.4 ± 3.9 a	21.5 ± 2.8 a	32.5 ± 5.6 b
Cover of shrubs (%)	2/21, 3.75, 0.0406	4.6 ± 1.0 a	6.3 ± 1.4 a	12.4 ± 2.8 b
Cover native forbs (%)	2/21, 3.25, 0.0590	36.8 ± 6.0 ab	28.6 ± 3.5 b	43.4 ± 2.8 a
Species with c.c. category 1 (%)[b]	2/21, 0.61, 0.5516	23.5 ± 2.0	21.3 ± 4.1	20.4 ± 3.8
Species with c.c. category 2 (%)[b]	2/21, 0.06, 0.9452	24.7 ± 2.8	23.4 ± 2.5	20.9 ± 5.3

[a] *Mixed-model analysis of variance is for treatment effects, with treatment as a fixed factor and treatment unit (n = 6 for burning treatment and grazing treatment, n = 12 for combined burning and grazing treatment) as a random factor. Significantly different treatment means are denoted by different letters (p < 0.1).*

[b] *Iowa coefficient of conservatism (c.c.) categories denote species dependence on unaltered habitat (1, least dependent; 2, most dependent).*

Table 3. Management goals and evaluation of burning and grazing treatments in a tallgrass prairie in western Iowa.

Management goal	*Evaluation*
Increase species diversity	grazing: greatest species richness, consistently most diverse for other metrics (not significant) burning and burning and grazing: similar (lower) diversity across metrics
Increase cover and diversity of native species	burning: greatest cover and richness of native species burning and grazing and grazing: similar (lower) cover and richness of native species
Decrease cover of woody, exotic, and cool-season grass species	burning and grazing and grazing: lowest cover of woody species (shrubs) burning: lowest cover of exotic and cool-season grass species
Promote conservative and uncommon native species	burning, burning and grazing, and grazing: similar proportion of conservative species, all three treatments promoted uncommon species, > 40% of uncommon species were unique to one treatment type

promoting both conservative and generalist species, it is possible that coefficients of conservatism were simply an ineffective metric in our evaluation of prairie management. Given the need for biological indicators of ecosystem integrity (Lopez & Fennessy 2002), more research is needed to better understand the utility of this commonly used metric for evaluating management success.

Because our study focused on an ongoing restoration effort, it represents an opportunity to assess how closely management outcomes mirror those of highly controlled field experiments. Field experiments are by definition based on precise timing and levels in the application of treatments. On the other hand, land managers are often understaffed and responsible for large areas, necessitating flexible restoration plans. We argue that past field experiments did not directly translate to effective management in our case, due to differences in species diversity and problems with exotic species (Collins 1987; Collins et al. 1998; Towne et al. 2005). That is not to say that controlled field experiments are not a valuable tool; these past studies were critical for our formulation of management goals and hypotheses. As our results demonstrate, it is important to evaluate how the two differ and what measures can be taken to reconcile discrepancies.

We suggest that one-size-fits-all management programs are unlikely to be effective for meeting diverse restoration goals. In our study each treatment best addressed at least one management goal; however, goals were often conflicting and no treatment accomplished all goals (Table 3). We suggest that at least two management approaches should be tested: grazing with targeted removal of problematic exotic species and burning with seeding/transplanting of desirable native species to increase overall diversity. Alternatively,

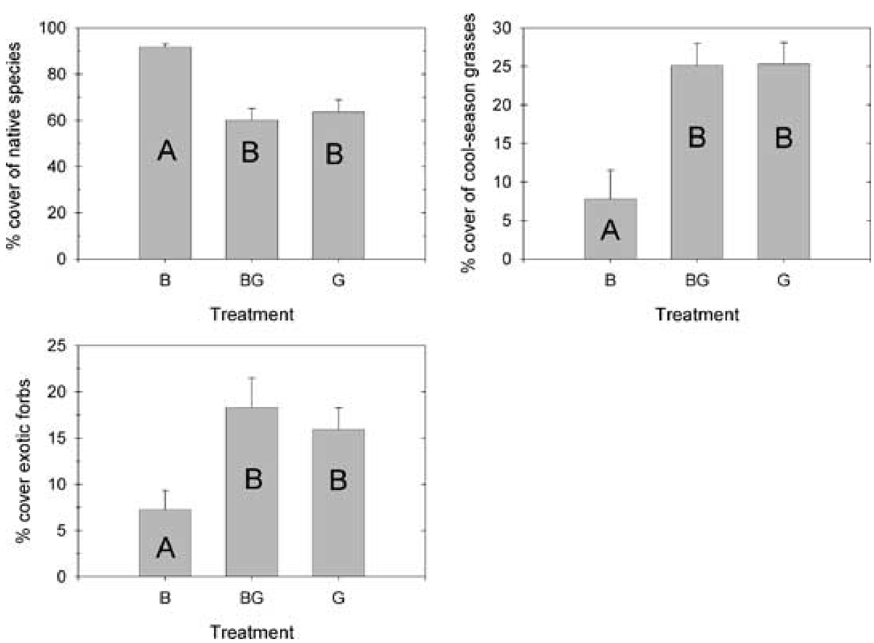

Figure 2. Percent cover of native species, cool-season grasses, and exotic forbs in 0.25-m^2 quadrats in a study of prairie management in western Iowa. Treatments were prescribed burning (B), burning with cattle grazing (BG), and cattle grazing (G). Bars represent means + 1 SE. Different letters on bars represent significant differences (independent linear contrast following ANOVA, $\alpha < 0.1$).

implementing a mosaic of management strategies may help accomplish multiple management objectives and allow for coexistence of a maximum number of desirable species on a single landscape. This approach might be most effective if managing for uncommon species is a major goal and exotic species' persistence is tolerable.

Although we recommend a species-specific approach to planning and assessing restoration success, we recognize that the intensive effort needed to understand how species will respond to management is unlikely to be feasible. Studies outside North America have identified groups of species that respond similarly to grazing due to shared life-history attributes, such as capacity for vegetative spread, seed dispersal, and shoot architecture (e.g., Noy-Meir et al. 1989; McIntyre et al. 1995). This life-history approach is used to avoid the need for species-specific studies, and such a framework could be applied to North American prairies. In a related approach Dornbush (2004) examined changes in the frequency of species over 50 years in an Iowa tallgrass prairie. A focus on habitat requirements of individual species allowed him to identify a group of species (those preferring xeric habitats) that declined in frequency over the period, most likely because management had shifted from mid-summer mowing for hay to regular spring burning. This pattern would have been missed in a diversity or life-form approach and led to a recommendation that management be diversified.

Conclusions

We suggest that multiple indexes, including species-specific responses, need to be considered during management planning and evaluation. Such an approach can best evaluate multiple, and possibly conflicting, goals and provide specific management recommendations to meet complex situations. Although many prairie species are uncommon generally and unevenly distributed (Howe 1995), it is important to consider uncommon species during this process (Lyons et al. 2005) so that management can best promote their landscape-scale persistence. Nevertheless, we recognize that it is not feasible to study every species in every ecosystem. Thus, it would be a fruitful application of diversity theory if one could recognize functionally similar species and apply these findings to management and conservation plans (Bestelmeyer et al. 2003).

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