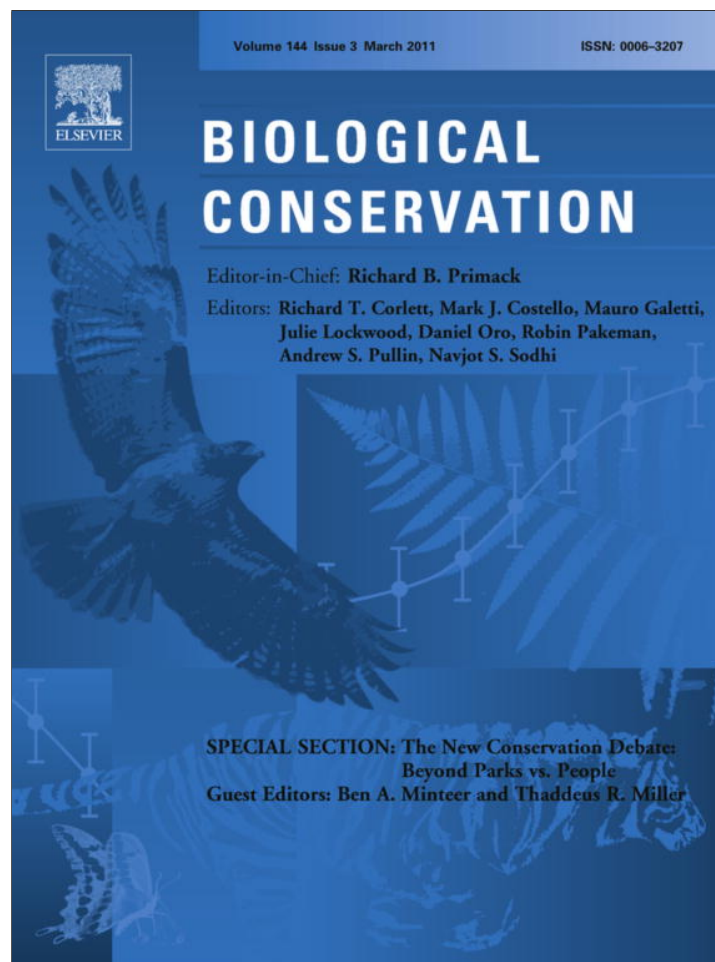




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Evaluating patterns of biodiversity in managed grasslands using spatial turnover metrics

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ABSTRACT

Market and policy incentives that encourage agricultural intensification, such as incentives for bioenergy, may contribute to biodiversity decline when they encourage a large-scale conversion of native and semi-natural ecosystems to production fields. In order to appreciate the impact of these incentives on biodiversity, it is imperative to better understand how native and semi-natural ecosystems contribute to plant diversity and composition. We studied the five most common types of managed grasslands in Northeastern Kansas, a region undergoing agricultural intensification. We analyzed plant community data recorded at three spatial scales in 98 managed grassland sites, and examined patterns of diversity and composition of plant species and functional groups; and spatial turnover of species and functional groups measured at different spatial scales. We found reduced soil quality and plant diversity as well as a lack of scale-dependent community patterns on sites that were historically cultivated. Forage management practices (hay or grazing) altered plant diversity and composition in native grassland remnants but not in non-native grasslands. We identified several opportunities where changes to existing management practices could benefit both conservation and bioenergy production objectives. Recommendations to conserve biodiversity include increasing the use of hay management or other biomass collection on native grassland remnants and improving the Conservation Reserve Program by increasing enrollment, adding more native species to seed mixes, and incorporating a periodic biomass collection. We also found that using measures of spatial turnover in community composition added important insights in understanding the effects of management decisions on biodiversity.

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1. Introduction

Conversion of native ecosystems to cropland and other land-uses has had dramatic impacts on biodiversity across the world (United Nations Environment Programme, 2007). Temperate grasslands are one of the most significantly impacted ecosystems by this land-use conversion (United Nations Environment Programme, 2007) due to their high quality soils that are suitable for crop production. For example, tallgrass prairie ecosystems in North America have been reduced to less than 1% of their original extent by conversion to cropland and non-native grasslands used for cattle forage (Samson and Knopf, 1994). The reduced extent of native grasslands has had negative impacts on habitat connectivity,

native biodiversity, and ecosystem function (Samson and Knopf, 1994).

Emerging market and policy incentives, including those for bioenergy production, are continuing the large-scale conversion of native, semi-natural, and non-native ecosystems to production fields (Fargione et al., 2008, 2009; Searchinger et al., 2008; Secchi et al., 2009). In the US, the ecosystems most at risk are in the corn belt (Secchi et al., 2009), which coincides with the tallgrass prairie region that has already been significantly altered. While existing native prairies are at risk of conversion to cropland, so are semi-natural forage production and Conservation Reserve Program (CRP) grasslands. The conversion of these ecosystems will likely lead to a loss of habitat for wildlife and increased habitat fragmentation (Fargione et al., 2009), but less is known about how it will affect plant biodiversity conservation.

Here, we study plant biodiversity patterns of semi-natural, managed grasslands in Northeastern Kansas, where corn and sorghum based ethanol production have recently increased. From 1984 to 2004, the area of corn planted increased from 187,000 to 479,000 acres (Kansas Agricultural Statistics Service, 2010). This region is characteristic of areas currently experiencing agricultural

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intensification and is ideal for studying biodiversity in managed ecosystems because its managed ecosystems are more ubiquitous than pristine native grasslands, and managed grasslands vary in their historical and contemporary land-use. We examine plant community patterns in grasslands managed for forage production or enrolled in the Conservation Reserve Program (Natural Resources Conservation Service, 2003). Some grasslands that are managed for forage production were historically plowed, used for row crops, and then planted with non-native C_3 grasses; whereas others are intact native tallgrass prairies dominated by native forbs and C_4 grasses. Currently, both native and non-native grasslands are managed for forage as either hay fields or cattle pastures. CRP sites are highly degraded from cultivation, and owners receive a subsidy from the US federal government to replant them with native perennial C_4 grasses (United States Department of Agriculture Farm Service Agency, 2007).

Here, we evaluate the effects of grassland management practices on diversity and composition of plant species and functional groups because these measures are important indicators of conservation value and habitat for wildlife (Brudvig et al., 2007; Foster et al., 2009; Haddad et al., 2001; Tilman et al., 2001; Weigelt et al., 2009). We expect historical and contemporary management practices to affect the species and functional composition of plant communities. Historical land-use change has replaced native, C_4 -dominated prairies with non-native, C_3 grasslands, causing a major shift in functional traits at the landscape scale. In addition, we expect contemporary management practices such as type of forage management to favor specific species or functional groups. We also compare the functional composition of restored, C_4 -dominated CRP grasslands to native, C_4 -dominated prairies to evaluate the utility of the CRP to restore plant functional diversity in this landscape.

We also examine the effect of management practices on patterns of spatial heterogeneity in plant species composition (hereafter referred to as spatial turnover) at several spatial scales. In native tallgrass prairies, analyses of spatial turnover at different scales have revealed the influence of environmental heterogeneity (e.g., soil gradients) on vegetation structure as well as the effects of disturbances associated with fire, ungulate grazing, and small-mammal activity (Collins, 1989, 1992; Collins and Smith, 2006; Gibson, 1989; Veen et al., 2008). For example, selective foraging decisions by native bison can increase spatial turnover at small scales due to variable grazing intensity among patches (Veen et al., 2008), whereas grazing can reduce spatial turnover at large scales by increasing dominance by C_4 grass species (Adler et al., 2001; Collins and Smith, 2006; Vinton et al., 1993). It is likely that the effect of management practices on patterns of spatial turnover may also vary with spatial scale of observation. For example, replanted grasslands on previously cultivated sites may have similar small and large scale turnover patterns due to a history of plowing, the uniform planting of perennial grass species, and the broad application of fertilizer and herbicide. We compare measures of spatial turnover to more traditional indicators used in ecosystem monitoring to see if spatial turnover provides a better understanding of how management practices alter community structure.

Our overall goal is to understand how management activities affect the plant species composition, spatial structure, functional group composition, and diversity of a landscape undergoing agricultural intensification. We use data recorded at four spatial scales in 98 privately managed grassland sites to evaluate differences in plant community structure as a function of grassland management practices. We examine patterns of diversity and composition of plant species and functional groups; and spatial turnover of species and functional groups measured at different spatial scales. Our results reveal the impacts of contrasting management activities on plant community structure and diversity and allow us to suggest

adaptive management practices that may enhance plant biodiversity in the region. We evaluate the potential for our recommendations to influence bioenergy production from agricultural and grassland ecosystems. In addition, we discuss the utility of measures of spatial turnover to improve the monitoring of biodiversity in managed and restored ecosystems.

2. Methods

2.1. Sampling

The study area is an agricultural region approximately 1500 km² in size and located at the prairie-forest ecotone of Northeastern Kansas in Jefferson, Leavenworth, and Douglas counties (39°N, 95°W; Fig. 1). Hay production and cattle grazing account for approximately 45% of the value of agricultural products from these three counties, and grain production (corn, soybeans, and wheat) accounts for the majority of agricultural products (Kansas Agricultural Statistics Service, 2010). All sites sampled were privately owned, were greater than or equal to one hectare in size, had upland topography, and had silt loam or silty clay loam soils. All suitable sites in the landscape were identified, but land-owner permission for access determined which sites were sampled. Here, we analyze data from a subset of sites originally published as a floristic study by Jog et al. (2006).

We selected 98 sites in five grassland management classes for sampling (Table 1), which represented the major grassland land-cover in the region: cool-season hay (C-H, 20 sites), cool-season grazed (C-G, 24 sites), warm-season native hay (W-NH, 18 sites), warm-season native grazed (W-NG, 17 sites), and warm-season Conservation Reserve Program (W-CRP, 19 sites). These management classes were based on historical and contemporary land-use. C-H and C-G sites were historically plowed, planted with crops, taken out of cultivation, and reseeded with non-native cool-season (C_3) grass species, most commonly *Bromus inermis* and *Schedonorus phoenix* (Kansas Agricultural Statistics Service, 2010). C-H and C-G sites are usually fertilized annually, whereas sites in other management classes are not fertilized. W-NH and W-NG sites are never-plowed tallgrass prairie remnants and are dominated by native warm-season (C_4) grasses and native forb species. Hay management on C-H and W-NH sites involves cutting and baling all plant material from the field during times of peak biomass: June for C-H and July for W-NH. Grazed sites are generally stocked with cattle during the growing season and allowed to rest during the dormant period. Spot-spraying of targeted weeds occurs in most management classes. Widespread spraying of woody and broadleaf herbicides is most common in C-H, C-G, and W-NG classes (C.A. Murphy, unpublished data).

W-CRP sites were historically plowed and cultivated for crop production. Under the original CRP, Kansas land-owners received a federal government subsidy to plant native warm-season grass species, which typically included *Andropogon gerardii*, *Bouteloua curtipendula*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. CRP sites in this region are required to be burned every few years to prevent woody encroachment. Other management activities are not permitted except in the case of extreme drought, when sites can be grazed (United States Department of Agriculture Farm Service Agency, 2007). Many sites in our study had been enrolled in the CRP for over 13 years. None were burned or grazed during the year of our study.

All 98 sites were surveyed from 26 May through 28 July 2004. In order to characterize the plant community at various spatial scales in each site, three replicates of nested quadrats were evenly distributed along a 100-m transect located in an upland, interior area. Nested quadrats measured three spatial grains: 1 m² (1 × 1 m),

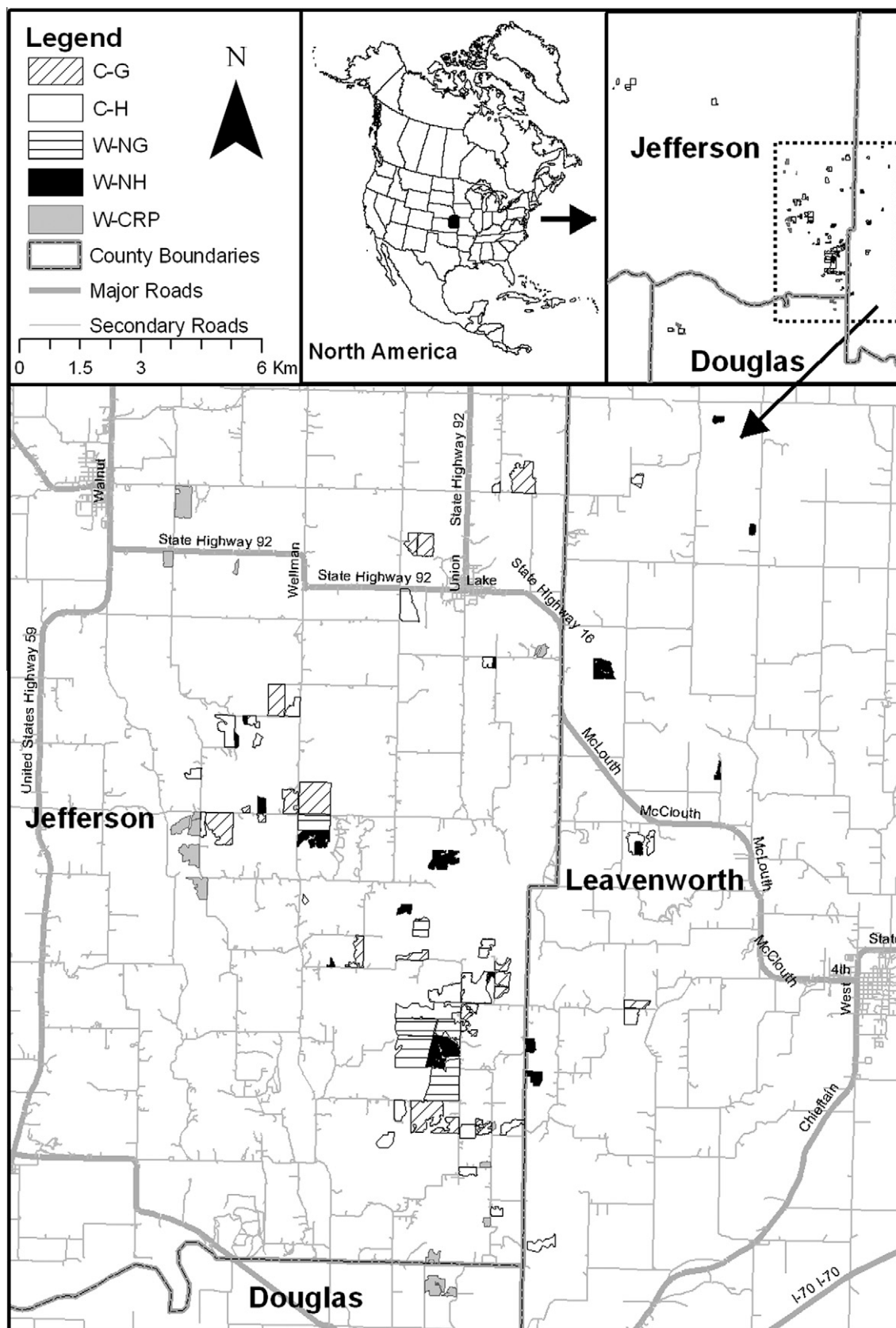


Fig. 1. Map of study area. Legend and scale correspond to detailed map, which shows the location of the majority of study sites coded by management class.

100 m² (10 × 10 m), and 400 m² (20 × 20 m). All plant species were recorded in each quadrat, and % cover for each species was

visually estimated in the 400-m² quadrats. To measure the soil quality of each 400-m² quadrat, three 150-mm deep soil samples

Table 1

Grassland management classes (C-H, C-G, W-NH, W-NG, and W-CRP) are based on whether the site was historically cultivated, and whether it is currently grazed, hay-managed, or enrolled in the Conservation Reserve Program.

Management class	Historical Management	Contemporary Management	Annual fertilization	Dominant plant cover
Cool-season grazed (C-G)	Plowed and cultivated	Grazing	Yes	Non-native C ₃ grasses
Cool-season hay (C-H)	Plowed and cultivated	Hay production	Yes	Non-native C ₃ grasses
Warm-season native grazed (W-NG)	Intact/native	Grazing	No	Native forbs and C ₄ grasses
Warm-season native hay (W-NH)	Intact/native	Hay production	No	Native forbs and C ₄ grasses
Warm-season Conservation Reserve Program (W-CRP)	Plowed and cultivated	Conservation/restoration	No	Planted native C ₄ grasses

were collected with a 914-mm tube sampler for pH and nutrient analysis. The three samples were mixed together and air dried at room temperature (22–27 °C) to a constant mass. Soils were sifted through a 2-mm sieve to remove roots and plant debris. Samples were sent to the Soil Testing Laboratory at Kansas State University where they were analyzed with a LECO CN 2000 dry combustion analyzer for total soil nitrogen and carbon (% by mass). We used a glass electrode pH meter to measure soil pH (McLean, 1982).

2.2. Functional group classification

In order to examine patterns of functional diversity and composition, each species was placed into a functional group on the basis of its longevity and growth form. We used published information to divide species into four longevity classes (annual, annual/biennial, biennial, and perennial) and 10 growth form classes (C₃ grass; C₄ grass; non-grass graminoid; C₃ forb; C₄ forb; shrub; vine; tree; leguminous forbs; and leguminous vines, shrubs, and trees) (Downton, 1975; Great Plains Flora Association, 1986; Towne, 2002; United States Department of Agriculture, 2009). We used all possible combinations of longevity classes with growth form classes to create 20 functional groups.

2.3. Data analysis

To characterize the diversity patterns for each site, we first calculated the relative abundance of each species in a site by adding its % cover from the three 400-m² quadrats and dividing that sum by the total vegetative cover from the three quadrats. These data were used to calculate site-level species richness (*S*), native species richness (*S_{Native}*), non-native species richness (*S_{Non-native}*), species evenness ($E = (1/\sum p_i^2)/S$), and Simpson's index of species diversity ($D = 1/\sum p_i^2$). We calculated the total relative abundance of native and non-native species to examine native and non-native cover, two important indicators of community integrity and ecosystem recovery following disturbance. The relative abundance of each functional group was determined in order to calculate site-level functional group richness (*S_{FG}*), functional group evenness (*E_{FG}*), and functional group diversity (*D_{FG}*). We calculated site-level metrics of soil quality (soil N, C, and pH) by averaging the three values of each measure from the 400-m² quadrats for each site. Because environmental heterogeneity can influence plant diversity, we examined the heterogeneity of soil conditions by calculating the coefficient of variation (CV) of soil N and C for each site.

We used two analysis of variance (ANOVA) models in Minitab 14.1 to test the effect of management class on site-level *S*, *E*, *D*, *S_{Native}*, *S_{Non-native}*, native cover, non-native cover, *S_{FG}*, *E_{FG}*, *D_{FG}*, soil N, soil C, soil pH, CV N, and CV C. One model was a one-way ANOVA using the five management classes as fixed factors. The other model was a two-way ANOVA omitting the W-CRP sites. The two factors were Historical Management (cultivated and replanted/not cultivated) and Contemporary Management (hay or grazing). By omitting the W-CRP sites from this analysis, we obtained a balanced design and could test for an interaction between Historical and Contemporary Management activities. If normality or homogeneity of variance assumptions were not met, we used a

Kruskal–Wallis test for one-way models and the Scheirer–Ray–Hare extension of the Kruskal–Wallis test for two-way models.

We used PERMANOVA, a non-parametric form of MANOVA, to test whether species and functional group composition varied among management classes (Anderson, 2001). PERMANOVA uses a community dissimilarity metric to evaluate differences in community composition among groups on a scale of zero (identical communities) to one (completely different communities) and employs permutation tests to evaluate significance. We tested one-way and two-way models similar to our ANOVA designs. We randomly selected sites to remove from each management class to obtain equal sample sizes among classes, a requirement for the analysis. We repeated the analyses three times, with different combinations of sites to ensure the results were repeatable. All tests used Bray–Curtis dissimilarity as the turnover metric and calculated *p*-values with 999 unrestricted permutations of the raw data. To graphically characterize the composition of sites, we performed separate Detrended Correspondence Analyses (DCA) in PC-ORD 4.14 for species and functional groups.

We used PERMDISP to determine whether spatial turnover among sites was greater in certain management classes (Anderson et al., 2006). PERMDISP finds the mean deviation of sites from the centroid for each management class and uses permutations to statistically evaluate differences in mean deviation from the centroid among classes. We ran PERMDISP analyses for species and functional group composition with 999 permutations and Bray–Curtis dissimilarity as the distance measure.

To test whether plant diversity patterns vary with spatial scale within sites, we calculated species richness (*S_S*) and functional group richness (*S_{FG}*) for each quadrat. We calculated the mean of each of these values over the three replicate quadrats of a given size in each site, resulting in three values of each metric for each site representing the mean for 1-m², 100-m², and 400-m² quadrat sizes. In order to test whether spatial turnover varied with spatial scale, we calculated spatial turnover (Sorensen's dissimilarity index) of species (*T_S*) and functional groups (*T_{FG}*) among all possible pairs of quadrats of each size in a site and found the mean spatial turnover for each quadrat size in each site.

We used a repeated-measures ANOVA in SPSS 14.0 to test whether the effect of management class on community patterns was scale-dependent. The repeated measure was sampling area (1 m², 100 m², and 400 m²) and management class was a fixed factor with five levels. A significant interaction term indicated that the effect of management on the dependent variable depended on spatial scale. We ran separate ANOVA's for *S_S*, *S_{FG}*, *T_S*, and *T_{FG}*. We log-transformed richness measures to allow for a more direct comparison of the effects of management among areas of different sizes.

3. Results

3.1. Site-level patterns

Over all sites we observed 390 species in 224 genera, 66 families, and 20 functional groups. Site-level *S* ranged from 7 to 108

Table 2
Comparisons of species, functional group, and soil productivity metrics among management classes. Mean $\pm$ 2SE are reported for each management class. Letters indicate significantly different groups based on Tukey post hoc tests of one-way ANOVA's ($p < 0.05$).

Dependent variable	C-G	C-H	W-NG	W-NH	W-CRP	Significant sources of variation ^a
<i>S</i>	33.9 $\pm$ 5.9 ^A	26.0 $\pm$ 4.9 ^A	77.6 $\pm$ 6.2 ^B	88.1 $\pm$ 5.9 ^B	46.0 $\pm$ 6.1 ^C	M, H, H $\times$ C
<i>E</i>	0.084 $\pm$ 0.02	0.077 $\pm$ 0.02	0.085 $\pm$ 0.01	0.080 $\pm$ 0.02	0.087 $\pm$ 0.01	
<i>D</i>	2.45 $\pm$ 0.37 ^A	1.72 $\pm$ 0.25 ^A	6.42 $\pm$ 0.78 ^B	6.99 $\pm$ 1.39 ^B	3.90 $\pm$ 0.63 ^C	M, H
<i>S</i> _{Native}	21.8 $\pm$ 4.10 ^A	16.0 $\pm$ 3.8 ^A	60.9 $\pm$ 6.14 ^B	73.1 $\pm$ 4.8 ^C	39.16 $\pm$ 5.0 ^D	M, H, H $\times$ C
<i>S</i> _{Non-native}	12.0 $\pm$ 2.7 ^{AB}	10.0 $\pm$ 1.9 ^{AD}	16.7 $\pm$ 1.9 ^C	14.9 $\pm$ 2.6 ^{BC}	6.8 $\pm$ 2.0 ^D	M, H
Native cover	8.34 $\pm$ 2.76 ^A	5.26 $\pm$ 2.18 ^A	79.12 $\pm$ 6.80 ^B	83.55 $\pm$ 6.16 ^B	97.20 $\pm$ 1.71 ^C	M, H
Non-native cover	91.7 $\pm$ 2.76 ^A	94.7 $\pm$ 2.18 ^A	20.8 $\pm$ 6.80 ^B	16.4 $\pm$ 6.16 ^B	2.8 $\pm$ 1.71 ^C	M, H
<i>S</i> _{FG}	10.8 $\pm$ 1.4 ^{AB}	9.0 $\pm$ 1.3 ^A	13.6 $\pm$ 0.9 ^C	12.6 $\pm$ 0.8 ^{BC}	12.8 $\pm$ 1.2 ^{BC}	M, H
<i>E</i> _{FG}	0.15 $\pm$ 0.03 ^{AB}	0.16 $\pm$ 0.03 ^{AB}	0.15 $\pm$ 0.02 ^{AB}	0.19 $\pm$ 0.03 ^B	0.11 $\pm$ 0.02 ^A	M, H, C
<i>D</i> _{FG}	1.46 $\pm$ 0.18 ^A	1.32 $\pm$ 0.18 ^A	2.00 $\pm$ 0.29 ^B	2.40 $\pm$ 0.41 ^B	1.33 $\pm$ 0.22 ^A	M, H, H $\times$ C
Soil N	0.24 $\pm$ 0.02 ^A	0.20 $\pm$ 0.02 ^B	0.26 $\pm$ 0.02 ^A	0.25 $\pm$ 0.02 ^A	0.16 $\pm$ 0.01 ^C	M, H, C
Soil C	2.59 $\pm$ 0.21 ^A	2.33 $\pm$ 0.20 ^A	3.07 $\pm$ 0.22 ^B	3.02 $\pm$ 0.20 ^B	1.81 $\pm$ 0.12 ^C	M, H
Soil pH	5.71 $\pm$ 0.18 ^A	5.72 $\pm$ 0.11 ^A	5.60 $\pm$ 0.14 ^{AB}	5.35 $\pm$ 0.11 ^B	5.86 $\pm$ 0.18 ^{AB}	M, H

^a One-way model: M = effect of Management Class; two-way model: H = effect of Historical management, C = effect of Contemporary Management, H $\times$ C = interaction of Historical and Contemporary Management. Significant sources of variation from one-way ANOVA's are reported for the effect of M on *S*, *S*_{Native}, and soil C, and from Kruskal–Wallis tests for the effect of Management Class on *S*_{Non-native}, native cover, non-native cover, *E*, *D*, *S*_{FG}, *E*_{FG}, *D*_{FG}, soil N, and soil pH. The effects of H and C were tested with a two-way factorial ANOVA for *S*, *S*_{Native}, *S*_{Non-native}, soil N, and soil C; and the Scheirer–Ray–Hare extension of the Kruskal–Wallis test for *E*, *D*, native cover, non-native cover, *S*_{FG}, *E*_{FG}, *D*_{FG}, and soil pH ($p < 0.05$).

species. Warm-season native sites had the greatest values of species and functional group diversity metrics analyzed at the site level (Table 2). Cool-season sites had the lowest *S*, *D*, and *S*_{FG}; W-CRP sites had intermediate values for these metrics. The Historical $\times$ Contemporary Management interaction was significant for values of *S* and *S*_{Native}, which occurred because grazed sites had lower values than hayed sites among warm-season grasslands, but grazed sites had values equivalent to hayed sites among cool-season grasslands (Table 2). W-CRP sites had the greatest native cover and lowest non-native cover, followed by warm-season native sites. Warm-season native sites had the greatest soil N and C (Table 2). W-CRP sites had the lowest N and C and the highest pH. There was no effect of Management Class, Historical Management, Contemporary Management, or the Historical $\times$ Contemporary Management interaction on *E* or soil heterogeneity variables, CV N and CV C ($p > 0.20$).

DCA of both species and functional groups provided clear separation of warm-season and cool-season sites on the first axis, which was highly influenced by dominant perennial grass species (Fig. 2). W-CRP sites were more closely associated with native sites, and were the farthest sites from cool-season sites on the first axis. W-NH and W-NG sites separated on the second species axis, but C-H and C-G sites did not. W-CRP sites were most closely associated with W-NG (Fig. 2a and b). W-NH and W-NG sites did not separate on the second axis when functional groups were analyzed (Fig. 2c and d).

PERMANOVA results supported these patterns. Each management class had a distinct species composition ($F_{4,80} = 23.35$, $p = 0.001$). Historical Management ($F_{1,64} = 65.69$, $p = 0.001$), Contemporary Management ($F_{1,64} = 3.52$, $p < 0.02$), and the Historical $\times$ Contemporary interaction term ($F_{1,64} = 2.56$, $p < 0.05$) all significantly affected species composition. In contrast, functional group composition was different between cool-season and warm-season sites (Historical Management $F_{1,64} = 106.24$, $p = 0.001$), but there was no effect of Contemporary Management ($F_{1,64} = 1.44$, $p > 0.05$) or the interaction term ($F_{1,64} = 1.69$, $p > 0.05$) on functional composition.

The spatial turnover in community composition among sites was related to management class (species: $F_{\text{PERMDISP}} = 7.06$, $p < 0.001$; functional groups: $F_{\text{PERMDISP}} = 5.62$, $p < 0.001$). Spatial turnover in species composition was highest among W-NG, W-NH, and C-G sites. Spatial turnover in functional group composition was highest among W-NH sites and lowest among W-CRP.

3.2. Spatial scale within sites

Management Class and Area were significant factors in ANOVA's of species richness (*S*_s), functional group richness (*S*_{FG}), species turnover (*T*_s), and functional group turnover (*T*_{FG}; Fig. 3). Even when measured at smaller spatial scales within sites, the patterns among management classes for *S*_s and *S*_{FG} richness were similar to the site-level patterns (i.e., W-NH had the greatest richness at all scales, followed by W-NG, etc.). The Area $\times$ Management interaction was significant for *S*_s ($F_{4,93} = 4.9$, $p < 0.001$), *S*_{FG} ($F_{4,93} = 13.9$, $p < 0.001$), and *T*_s ($F_{4,93} = 6.204$, $p < 0.001$; Fig. 3). This interaction did not occur for *T*_{FG} ($F_{4,93} = 0.79$, $p > 0.05$). For *S*_s and *S*_{FG} there was a greater difference among management classes at small scales compared to large scales. In contrast, the interaction between management class and area occurred for *T*_s because the rank of management classes changed with spatial scale. *T*_s of warm-season sites was higher than other management classes at the 1-m² scale but was lower or equivalent at the 400-m² scale (Fig. 3). *T*_{FG} of cool-season and W-CRP sites was greater than or equivalent to warm-season sites at all spatial scales.

4. Discussion

4.1. Managed tallgrass prairies

The management of prairie remnants for forage production appears to help retain native plant diversity in this region (Jog et al., 2006). The average species richness at the 1-m² scale of grazed native grasslands (15 species) equaled the richness of a nearby prairie remnant managed exclusively for conservation; and the richness of hay-managed native grasslands (23 species) exceeded the remnant's richness (Kindscher and Tieszen, 1998). The scale-dependent patterns of species turnover we observed for grazed and hayed native grasslands are similar to those found at Konza prairie, a tallgrass prairie managed for conservation, suggesting that prairies managed for forage production can maintain important elements of community structure found in high quality native prairie ecosystems (Adler et al., 2001; Collins and Smith, 2006; Veen et al., 2008; Vinton et al., 1993). It is remarkable that these remnants have such high diversity even though the sites are small, isolated, and managed for forage production. Most of these sites exist because they were too rocky to plow or were otherwise unsuitable for crop production, so it is possible that they will

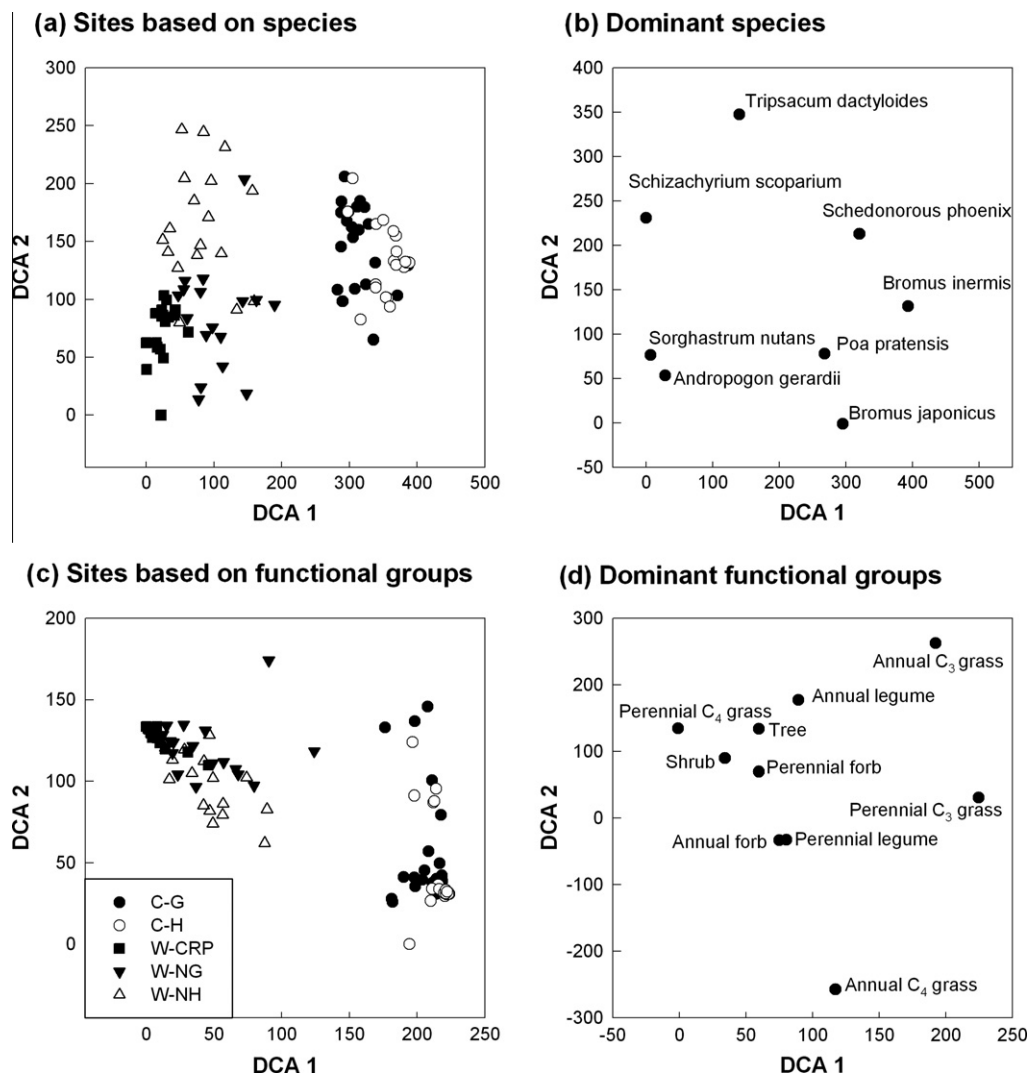


Fig. 2. Detrended correspondence analysis axes 1 and 2. Sites are coded by management class. (a) Species ordination: the first axis explained 60.8% of the variation in site composition, and the second axis explained an additional 5.9%; (b) dominant species with >50% cover; (c) functional group ordination: the first axis explained 93.1% of the variation in site composition, and the second axis explained an additional 1.4%; (d) dominant functional groups with >10% cover.

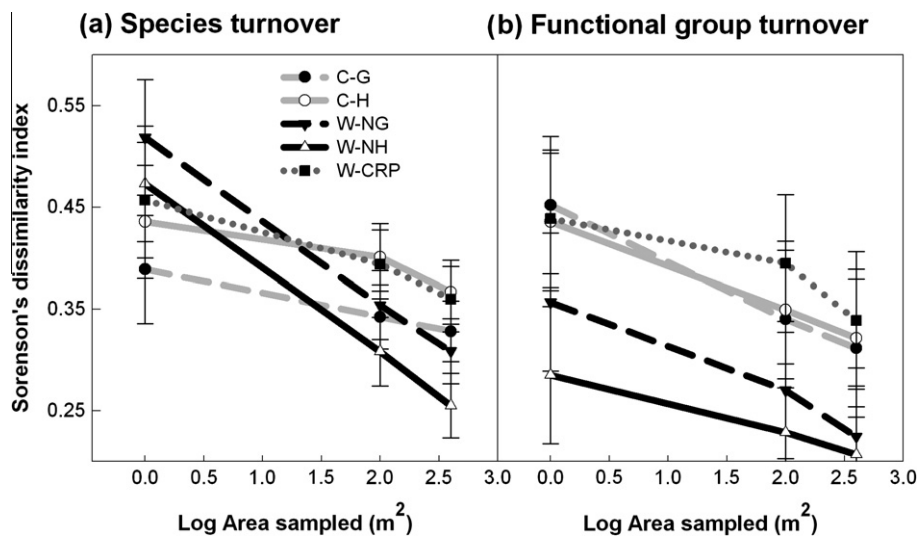


Fig. 3. Spatial turnover for each area sampled by management class. Symbols represent mean turnover $\pm 2SE$ plotted against log area. (a) Species turnover; (b) functional group turnover.

remain intact even if pressures for arable land continue to increase. However, if bioenergy crops become more profitable some of these sites may be converted to agricultural fields. Financial and policy incentives that focus on preventing this land-use conversion will have the greatest impact on native plant diversity in this region.

4.2. Contemporary forage management practices

We found evidence that contemporary forage management practices (annual haying and grazing by cattle) influenced plant diversity and composition in native grasslands, but not in non-native cool-season grasslands. Native grasslands managed for cattle grazing had lower native species richness when compared to native grasslands managed to produce hay. PERMANOVA results showed that W-NH sites had a different species composition from W-NG sites, but their functional group composition was similar. Thus, grazing management may reduce species richness in native grasslands by eliminating native species that cannot tolerate cattle grazing but are adapted to hay disturbance, but not by eliminating entire functional groups (Towne et al., 2005). Possible causes of species loss in grazed sites include high stocking rates of cattle that lead to soil erosion, high rates of disturbance that negatively affect certain species, and herbicide application to eliminate specific unpalatable plants.

The community differences among W-NH and W-NG sites suggest that contemporary management practices can play a role in maintaining diversity in native grasslands, and that hay management in particular may be an important tool for native plant conservation. Mead's milkweed, a federally endangered plant species, is found only in hay-managed grasslands and not in grazed grasslands in this region (Jog et al., 2006). In addition, the nesting success of grassland birds was higher in native hay meadows compared to grazed prairies or Conservation Reserve Program (CRP) grasslands, suggesting that hay management also improves wildlife habitat quality (With et al., 2008). Mowing may be a lower intensity disturbance, when compared to cattle grazing, that benefits soil quality and species of conservation concern (Knapp et al., 1999; Leach et al., 1999). In addition, mid-season hay management may approximate the prehistoric fire disturbance to which these native tallgrass communities have adapted (Howe, 1994a,b). Therefore, switching from grazing to hay management could enhance the community composition of native grasslands. We also suggest exploring the effects on biodiversity of reducing stocking densities, resting sites in order to reduce erosion, temporarily switching grazed sites to hay management, or rotating hay management through portions of grazed sites.

Although reducing grazing activity may decrease an owner's revenue, this loss could be mitigated by market or policy incentives for bioenergy derived from native or semi-natural biomass. These incentives could also provide a unique opportunity to alter the timing of hay collection. Currently, hay is harvested when its forage quality is greatest, which is normally mid-growing season before plants set seed and senesce (Foster et al., 2009). Since bioenergy production does not rely as heavily on the nutrient status of plants, biomass could be collected later in the season after plant and animal species have an opportunity to reproduce. Thus, bioenergy produced from these ecosystems could potentially enhance biodiversity by reducing the negative impacts of grazing and altering the timing of hay collection to facilitate plant and animal reproduction.

4.3. Conservation Reserve Program grasslands

Despite their history of intensive cultivation, CRP grasslands had greater species diversity and native cover than cool-season grasslands. In addition, the species and functional group composi-

tion of CRP sites was more similar to native grasslands than the composition of cool-season grasslands was. This similarity reflects the influence of dominant grass species on composition, showing that some aspects of native community structure can be restored through simple seed additions of native warm-season grasses. Native species richness of CRP grasslands was considerably higher than the five species initially planted (39 ± 5 species) and was approximately twice as high as native richness of cool-season grasslands. Thus, CRP grasslands have created important reservoirs of native plant diversity and restored some aspects of functional composition to previously cultivated sites in this intensively farmed landscape.

However, CRP grasslands do not achieve the same diversity and composition of native grasslands. The species richness of CRP grasslands is low compared with native grasslands, similar to comparisons of restored and remnant prairies in Iowa and Texas (Martin et al., 2005; Polley et al., 2005). CRP grasslands also lacked scale-dependent patterns of species turnover within sites and at the landscape scale. CRP sites had higher small-scale functional group turnover compared to native prairies, which may occur when patches of individual species or functional groups are larger in restorations (Martin et al., 2005). Low diversity in CRP grasslands is caused primarily by the initial extirpation of native diversity when these sites were plowed and planted with row crops. Typical CRP restoration activities, such as planting dominant C₄ grasses and maintaining grass dominance by eliminating natural or managed disturbance regimes (Knapp et al., 1998) also limit the diversity of these grasslands.

We suggest three modifications to management practices that may increase species richness, reduce grass dominance, and improve the ability of CRP grasslands to resemble native communities. First, increasing enrollment in the CRP will increase native species diversity at the landscape scale by increasing the area of favorable native plant habitat, reducing the abundance of non-native species, and reducing habitat fragmentation if sites are strategically placed in the landscape (Dunn et al., 1993). Incentives could also be added to convert cool-season grasslands, in addition to cropland, to native warm-season CRP management. Second, increasing incentives through the CP25 Restoration of Rare and Declining Habitats Program will include more native prairie species in seed mixes, especially forbs and native cool-season grasses (Dickson and Busby, 2009; Martin et al., 2005; Natural Resources Conservation Service, 2010; Polley et al., 2005). Current applications for CRP enrollment receive higher scores if they include CP25 management, a positive step toward enhancing restored plant diversity. Third, incorporating a periodic biomass collection may enhance native species diversity on CRP sites by reducing the dominance of perennial C₄ grasses. If this biomass collection can be used to produce bioenergy, CRP grasslands could have both a market and conservation value. However, removing vegetation from CRP sites may change wildlife habitat quality, reduce litter decomposition, and cause an undesirable reduction in soil nutrients (Kitchen et al., 2009; Knops and Tilman, 2000; Murphy et al., 2006), particularly carbon, which could reduce the soil carbon sequestered by CRP management. Therefore, careful study is needed to determine the impacts of management changes to the CRP on soil processes, wildlife, and other functions; and to understand the optimal frequency and timing of biomass collection for both biodiversity and soil conservation.

4.4. Spatial turnover indicators for ecological monitoring

Comparing managed and restored communities to reference native ecosystems is an important aspect of biodiversity monitoring. Native species richness, native cover, non-native cover, or the abundance of target species are typical indicators used for

monitoring plant community responses to management activities (Yoccoz et al., 2001). In our study, CRP grasslands had very high native cover, low non-native cover, and moderate species richness; exhibiting a level of similarity to native grasslands; however, CRP grasslands did not exhibit scale-dependent patterns of spatial turnover measured within sites or at the landscape scale. In fact, the very high cover of planted native grasses, which may seem an ideal target for restoration, may inhibit natural patterns of spatial turnover on CRP sites by increasing grass dominance over levels found in native grasslands (Martin et al., 2005). Thus, we have gained a better understanding of management impacts to community structure at multiple scales by analyzing patterns of spatial turnover. These metrics are not typically included in monitoring protocols, but are easy to calculate with sufficient data. We suggest that these metrics can be used to evaluate the effectiveness of restoration and conservation activities in many ecosystems. In particular, examining spatial turnover at the landscape scale using PERMDISP or other analytical approaches can benefit landscape-level biodiversity management (e.g., Anderson and Thompson, 2004).

5. Conclusions

Changes to management practices could significantly enhance biodiversity conservation in regions where agricultural intensification is accelerating land-use change. In our study region, we suggest native plant biodiversity can be enhanced by conserving existing native grasslands, increasing the conversion of cropland to native CRP grasslands, and increasing the use of hay management in native pastures. Our study emphasized managed temperate grassland ecosystems, and our management recommendations may not be suitable for unmanaged, natural areas; however, we think many of our suggestions could have positive effects on biodiversity in other grassland regions. Furthermore, indicators based on measures of spatial turnover in community composition added important insights when monitoring the effects of management decisions on biodiversity, and may be important for understanding landscape change in other ecosystems.

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References

Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* (Berlin) 128, 465–479.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9, 683–693.

Anderson, M.J., Thompson, A.A., 2004. Multivariate control charts for ecological and environmental monitoring. *Ecological Applications* 14, 1921–1935.

Brudvig, L.A., Mabry, C.M., Miller, J.R., Walker, T.A., 2007. Evaluation of central North American prairie management based on species diversity, life form, and individual species metrics. *Conservation Biology* 21, 864–874.

Collins, S.L., 1989. Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. *Vegetatio* 85, 57–66.

Collins, S.L., 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology* 73, 2001–2006.

Collins, S.L., Smith, M.D., 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87, 2058–2067.

Dickson, T.L., Busby, W.H., 2009. Forb species establishment increases with decreased grass seeding density and with increased forb seeding density in a Northeast Kansas, USA, experimental prairie restoration. *Restoration Ecology* 17, 597–605.

Downton, W.J.S., 1975. The occurrence of C_4 photosynthesis among plants. *Photosynthetica* 9, 96–105.

Dunn, C.P., Stearns, F., Guntenspergen, G.R., Sharpe, D.M., 1993. Ecological benefits of the conservation reserve program. *Conservation Biology* 7, 132–139.

Fargione, J., Hill, J., Tilman, D., Polasky, S., Hawthorne, P., 2008. Land clearing and the biofuel carbon debt. *Science* 319, 1235–1238.

Fargione, J.E., Cooper, T.R., Flaspohler, D.J., Hill, J., Lehman, C., McCoy, T., McLeod, S., Nelson, E.J., Oberhauser, K.S., Tilman, D., 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. *Bioscience* 59, 767–777.

Foster, B.L., Kindscher, K., Houseman, G.R., Murphy, C.A., 2009. Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecological Applications* 19, 1884–1896.

Gibson, D.J., 1989. Effects of animal disturbance on tallgrass prairie vegetation. *American Midland Naturalist* 121, 144–154.

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

Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M., Knops, J.M.H., 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* 158, 17–35.

Howe, H.F., 1994a. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology* 8, 691–704.

Howe, H.F., 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications* 4, 121–133.

Jog, S., Kindscher, K., Questad, E.J., Foster, B., Loring, H., 2006. Floristic quality as an indicator of native species diversity in managed grasslands. *Natural Areas Journal* 26, 149–167.

Kansas Agricultural Statistics Service, 2010. *Kansas Agricultural Statistics*.

Kindscher, K., Tieszen, L.L., 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology* 6, 181–196.

Kitchen, D.J., Blair, J.M., Callahan, M.A., 2009. Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie. *Plant and Soil* 323, 235–247.

Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L., 1998. *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie*. Oxford University Press.

Knapp, A.K., Hartnett, D.C., Collins, S.L., Briggs, J.M., 1999. A caution against grazing – response. *Bioscience* 49, 600–601.

Knops, J.M.H., Tilman, D., 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81, 88–98.

Leach, M.K., Henderson, R.A., Givnish, T.J., 1999. A caution against grazing. *Bioscience* 49, 599–600.

Martin, L.M., Moloney, K.A., Wilsey, B.J., 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* 42, 327–336.

McLean, E.O., 1982. Soil pH and lime requirement. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties*. American Society of Agronomy, Madison, WI, pp. 200–209.

Murphy, C.A., Foster, B.L., Ramspott, M.E., Price, K.P., 2006. Effects of cultivation history and current grassland management on soil quality in Northeastern Kansas. *Journal of Soil and Water Conservation* 61, 75–84.

Natural Resources Conservation Service, 2003. *National Resources Inventory, Land Use*. United States Department of Agriculture.

Natural Resources Conservation Service, 2010. *CRP Practice CP25: Restoration of Rare and Declining Habitat Program Fact Sheet*. United States Department of Agriculture.

Polley, H.W., Demer, J.D., Wilsey, B.J., 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. *Restoration Ecology* 13, 480–487.

Samson, F., Knopf, F., 1994. Prairie conservation in North America. *Bioscience* 44, 418–421.

Searchinger, T., Heimlich, R., Houghton, R.A., Dong, F.X., Elobeid, A., Fabiosa, J., Tokgoz, S., Hayes, D., Yu, T.H., 2008. Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* 319, 1238–1240.

Secchi, S., Gassman, P.W., Williams, J.R., Babcock, B.A., 2009. Corn-based ethanol production and environmental quality: a case of Iowa and the conservation reserve program. *Environmental Management* 44, 732–744.

Tilman, D., Reich, P., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845.

Towne, E.G., Hartnett, D.C., Cochran, R.C., 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* 15, 1550–1559.

Towne, G.E., 2002. *Vascular plants of Konza Prairie biological station: an annotated checklist of species in a Kansas tallgrass prairie*. SIDA Contributions to Botany 20, 269–294.

United Nations Environment Programme, 2007. *Global Environment Outlook 4: Environment for Development*.

United States Department of Agriculture, 2009. *The PLANTS Database*. National Plant Data Center, Baton Rouge, LA 70874-4490, USA.

United States Department of Agriculture Farm Service Agency, 2007. *Conservation Programs*.

Veen, G.F., Blair, J.M., Smith, M.D., Collins, S.L., 2008. Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. *Oikos* 117, 859–866.

- Vinton, M.A., Hartnett, D.C., Finck, E.J., Briggs, J.M., 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *American Midland Naturalist* 129, 10–18.
- Weigelt, A., Weisser, W.W., Buchmann, N., Scherer-Lorenzen, M., 2009. Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences* 6, 1695–1706.
- With, K.A., King, A.W., Jensen, W.E., 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141, 3152–3167.
- Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16, 446–453.