



# Management of remnant tallgrass prairie by grazing or fire: effects on plant communities and soil properties

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**Citation:** Larson, D. L., D. L. Hernández, J. L. Larson, J. B. Leone, and N. Pennarola. 2020. Management of remnant tallgrass prairie by grazing or fire: effects on plant communities and soil properties. *Ecosphere* 11(8):e03213. 10.1002/ecs2.3213

**Abstract.** Tallgrass prairie is a disturbance-dependent ecosystem that has suffered steep declines in the midwestern United States. The necessity of disturbance, typically fire or grazing, presents challenges to managers who must apply them on increasingly small and fragmented parcels. The goal of this study was to compare effects of management using cattle grazing or fire on vegetation and soil characteristics to aid managers in making decisions regarding the kind of disturbance to apply. We selected 73 sites, of which 27 were managed solely by cattle grazing and 46 solely by fire, for at least 11 yr leading up to the study. We stratified the sites by prairie type (dry, mesic, and wet) and sampled frequency of plant species on randomly placed transects, supplemented with botanist-directed walks, and collected and composited five soil cores on a randomly selected transect within each prairie type at each site. We calculated rarefied richness and Shannon evenness from the transect data and mean coefficient of conservatism (CofC) from the total list of species. Soil samples were analyzed for texture, bulk density, total N and C, and potential net N nitrification and mineralization. A nonmetric multidimensional scaling analysis of the plant community data revealed differences in species associated with mesic and wet prairies, but no separation by management type. Similarly, none of the vegetation variables we calculated varied by management type, as determined by mixed-effects models, but soil bulk density was 17.5% higher and total N was 22% higher on grazed sites than burned sites. Sites burned more recently had higher species richness and mean CofC, but fire was not associated with any soil variables. Sites grazed more recently had higher bulk density, total N and C, and faster N cycling rates. Overall, 28% of plant species were found exclusively in one management type or the other, but these species did not vary in mean CofC. We conclude that, at the levels of burning and grazing intensity we studied, both management approaches produce similar C storage and vegetation responses. To maintain maximum diversity across the landscape, however, both approaches are necessary.

**Key words:** *Bromus inermis*; carbon sequestration; coefficient of conservatism; grassland; nitrogen cycling; plant species richness; *Poa pratensis*.

**Received** 21 January 2020; revised 4 March 2020; accepted 11 May 2020; final version received 5 June 2020. Corresponding Editor: Debra P. C. Peters.

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## INTRODUCTION

Remnant tallgrass prairies are vanishingly rare components of the midwestern U.S. landscape, and proper management is necessary to ensure their persistence and ability to maintain biodiversity and ecological functioning. Remnant prairies are those that have remained unplowed and unconverted to agriculture. However, this does not imply they have escaped anthropogenic effects. Fragmentation, nitrogen (N) enrichment, and encroachment by invasive species are just a few of the impacts that can change plant and soil characteristics, and ultimately ecosystem function, of remnant tallgrass prairies.

Managers rely on thoughtfully applied disturbance to prevent remnant prairie degradation due to woody encroachment, exotic species invasion, and litter accumulation; two of the most commonly used disturbances are prescribed fire and grazing by domestic cattle. Both fire (naturally occurring and anthropogenic) and grazing by native ungulates were integral to the formation and persistence of prairies since long before European settlement (Howe 1999, Allred et al. 2011, Middleton 2013), and current management approaches aim to mimic these natural processes at the much smaller scale of prairie remnants. Historically, tallgrass prairie experienced burning and grazing in a shifting mosaic of disturbance (Anderson 2006, McGranahan et al. 2012). Lacking disturbances such as these, tallgrass prairie may transition to woodland (Brunsell et al. 2017) or be overrun by non-native invasive cool-season grasses (DeKeyser et al. 2013), fates that alter ecosystem function and reduce habitat quality for a variety of prairie-dependent species, including many pollinators. Due to their small size, modern prairies rarely experience both burning and grazing by large ungulates. Instead, managers choose the action that is the most logistically or economically feasible for a given prairie and often apply that single management strategy over the long term, though it is more common for grazed prairies to be occasionally burned than the inverse due to lack of infrastructure for grazers.

As prairie remnants become smaller and more isolated, the use of these management approaches becomes more costly and more challenging. Prescribed burning must be performed

on smaller, more numerous parcels, and prescriptions must account for smoke production and the direction it will travel to avoid busy roadways and housing developments. While it has always been important to ensure that a prescribed fire does not escape, the implications of escape are increasingly serious as the exurban human population increases (Toledo et al. 2013). It is also difficult to provide refuges from fire for creatures that lack mobility to flee, especially in small remnants (Henderson et al. 2018). These considerations limit the timing and intensity of prescribed fires, which can influence ecosystem effects (e.g., Howe 1995, Twidwell et al. 2013). These concerns take precedence over such goals as timing a fire to best control invasive species and therefore reduce fire's effectiveness in achieving management objectives. Grazing with domestic cattle has fewer off-site effects, as cattle are confined to specific predetermined areas. Nonetheless, adequate fencing, access to water and minerals, and partnerships with livestock owners who are willing to abide by conservation goals can be obstacles to managers of conservation lands who would apply grazing management.

Decisions on how to manage individual remnants are based on likelihood of achieving management objectives, assuming the manager can overcome logistical constraints like those described above. Management effects are highly contingent on environmental conditions at the time management occurs, which limits generalization among geographically and temporally distant studies (Jonas et al. 2015). For example, a wealth of knowledge has been generated by long-term studies on tallgrass prairies at Konza Prairie in the Flint Hills of Kansas, USA, but applicability to the different environmental and management conditions in the northern tallgrass prairies of the upper Midwest must be tested (Symstad and Jonas 2011). The results of prescribed fire may vary depending on the local conditions that limit diversity: moisture stress in western tallgrass prairies vs. reduced light availability due to canopy closure in northern tallgrass prairies (Bowles and Jones 2013); such variation in limiting conditions likely also plays a role in effects of grazing (Xu et al. 2018a).

Both periodic fire and moderate grazing can limit dominance and decrease thatch

accumulation, thereby allowing the vegetation to express greater diversity by decreasing competition for subordinate species and increasing light availability to small-statured species (Leach and Givnish 1996, Knapp et al. 1999, Bond and Keeley 2005, Collins and Calabrese 2012). In Flint Hills tallgrass prairies, bison have been shown to selectively graze the dominant grasses, thus increasing forb abundance and overall diversity (Towne et al. 2005, Elson and Hartnett 2017). Although foraging ecology of cattle and bison differs (Plumb and Dodd 1993, Damhoureyeh and Hartnett 1997, Allred et al. 2011), perhaps as a result of differences in how they are managed (Towne et al. 2005), similar reduction in dominant grasses and increased diversity were found in Oklahoma (Collins 1987) and Kansas (Towne et al. 2005) grazed tallgrass prairies compared to ungrazed prairies. Brudvig et al. (2007) found that neither burning nor grazing optimized response to all of the management objectives in the Iowa Loess Hills; burning better controlled invasive cool-season grasses but grazing favored certain desired uncommon species. Responses of higher trophic levels to fire and grazing may not be tightly linked to their effects on vegetation, however. For example, Leone et al. (2019) found greater monarch butterfly abundance in burned than grazed tallgrass prairie sites in Minnesota, even though forb and host-plant frequencies did not differ. In general, spatially and temporally variable management approaches are recommended to maximize grassland biodiversity by increasing habitat heterogeneity, regardless of the type of management tool applied (Anderson 2006, Brudvig et al. 2007).

Grazing and fire can both affect belowground processes in prairie (Johnson and Matchett 2001), but there are few studies that directly compare the effects of these two management actions on soil characteristics. The effect of burning and grazing on bulk density, nutrient availability, and carbon (C) sequestration is dependent on several factors, including the frequency, intensity, and duration of the disturbance and productivity potential of the system (Seastedt et al. 1991, McSherry and Ritchie 2013, Andrés et al. 2017, Byrnes et al. 2018). Of concern to land managers are bulk density, which affects soil compaction and water infiltration; N cycling, which reduces resource availability for invasion as cycles slow;

and C stocks, which directly relate to sequestration of an important greenhouse gas. The association of grazing intensity with increasing bulk density has been demonstrated repeatedly (Byrnes et al. 2018, Xu et al. 2018b), but any effect of fire on bulk density seems only to occur via changes in vegetation (Hester et al. 1997). Effects of bulk density on vegetation management objectives revolve around changes in soil drainage characteristics, especially in the rooting zone of plants, and seedling emergence (Assouline 2006). Grazing and burning also may have unique effects on N cycling and C sequestration. Burning indiscriminately removes aboveground plant biomass, volatilizing C and some nutrients from the plant tissue and depositing remaining nutrients in ash. A single burn event often increases nutrient availability (Wan et al. 2001) and productivity (Hulbert 1988). However, long-term frequent fires can reduce soil nutrient availability over time as the nutrients are lost through volatilization and leaching (Ojima et al. 1994, Hernandez and Hobbie 2008). Frequent burning in prairie can lead to net ecosystem C loss, but the magnitude of this effect is influenced by precipitation in years following fire (Bremer and Ham 2010). In contrast to burning, grazing selectively reduces the biomass of preferred species, leaving unpalatable species with reduced competition for light and nutrients. Grazers convert plant nutrients into more labile forms via waste deposition, potentially accelerating rates of nutrient cycling. The intensity and duration of grazing, along with the productivity potential of the system, interact to determine the direction and magnitude of grazing effects on C sequestration (McSherry and Ritchie 2013).

We tested the hypothesis that the management of remnant prairies with grazing vs. burning for at least 11 yr results in prairies with different plant community and soil characteristics. Effects of management actions may take many years or even decades to become evident in ecosystems such as tallgrass prairie dominated by perennial plants (Wagle and Gowda 2018). For this reason, we evaluated response variables on remnant prairies that have been subject to either fire or grazing over at least 11 yr prior to surveys. Our sample sites included prairies managed only for conservation as well as some privately owned prairies where the objective was livestock

production, but with the recognition that prairie conservation was important for sustainable production. If, contrary to our hypothesis, fire and grazing can be used to achieve comparable results, prairies managed by fire and those managed by grazing should be similar in terms of native plant community composition; species richness, evenness, and conservatism (i.e., mean coefficient of conservatism [CofC]); and resistance to invasive grasses. Changes in soil characteristics may be due to the direct effects of management actions on soil (e.g., the effect of grazers on soil bulk density or the effect of burning on soil nutrient availability) or arise indirectly as management actions change plant community composition and plant functional traits. However, if burning and grazing are functionally equivalent management actions, we would expect to see no difference in soil characteristics with respect to management approach.

## MATERIALS AND METHODS

### *Study site selection*

Candidate sites for the study were all remnant prairies in the Prairie Parkland Province in western Minnesota that we could confirm had been managed solely by grazing or by fire between 2005 and 2015. Of these, we selected 73 sites representing a range of sizes (1.13–144.7 ha) and management intensity (0.99–7.19 animal unit months [AUM] per ha; 0.4–2.91 AUM per acre and 2–11 yr when grazing was applied; or 1–4 fires over the 11-year period prior to sampling). Because grazing is a less commonly used management tool than fire in Minnesota, we identified only 27 sites that were grazed (comprising 1 dry, 21 mesic, and 16 wet prairies; more than one prairie type could occur at a site) but 46 sites that were burned (comprising 3 dry, 35 mesic, and 30 wet prairies; Fig. 1, Table 1). We stratified sampling by prairie type because we expected different plant communities to be associated with soil moisture regime. Prairies we classified as dry fell into the Natural Resources Conservation Service drainage classes excessively and somewhat excessively drained; mesic prairies were well, moderately well, and somewhat poorly drained; and wet prairies were poorly or very poorly drained (<http://websoilsurvey.nrcs.usda.gov/>). Ownership of prairies included U.S. Fish and

Wildlife Service, Minnesota Department of Natural Resources, the Nature Conservancy, and private landowners; all required permits and permissions were secured prior to sampling.

### *Sampling design and data layers*

Prior to the field season, we created a GIS map that delineated soil type within each candidate remnant prairie site. Water retention properties of the soil types were used to stratify sampling within sites so that all potential prairie types (wet, mesic, and dry) were sampled within sites. The experimental units were the grazed or burned prairies (an area subjected to one management regime, hereafter “site”), and the polygons of wet, mesic, and dry prairie types within a site were subplots (for statistical purposes). Within each polygon created by prairie type and management unit boundaries, we estimated frequency by species on 0.5 × 2-m plots located on randomly placed transects that ran from edge to edge of the prairie type through random points (Fig. 1). Transects were delineated on maps prior to the field season to run parallel to any elevation gradient; if no gradient existed, a random number table was used to select a compass bearing for transect orientation. Plots were oriented perpendicular to the transects, which ranged in length from 36 to 1058 m; transect length was dependent on size and shape of the prairie type within the management unit. The number of plots per site ( $n$ ) was proportional to the size of the site (not the prairie types within the site), with a minimum of 5 and an asymptote at 30 plots, per the following equation:

$$n = a \times (1 - \exp(-b \times x))$$

where  $a = 30$  and  $b = 0.163$  and  $x$  is the size of the site in ha.

These plots were distributed on transects in proportion to the area of each prairie type within the site. Plots were placed at least 10 m from the ends of the transects and equidistant from each other within the transect. The starting and ending points of the transects were stored on handheld GPS units for use in the field.

### *Vegetation field methods*

Each study site was visited once in either 2016 or 2017. We recorded the presence of each species detected within each plot and from this

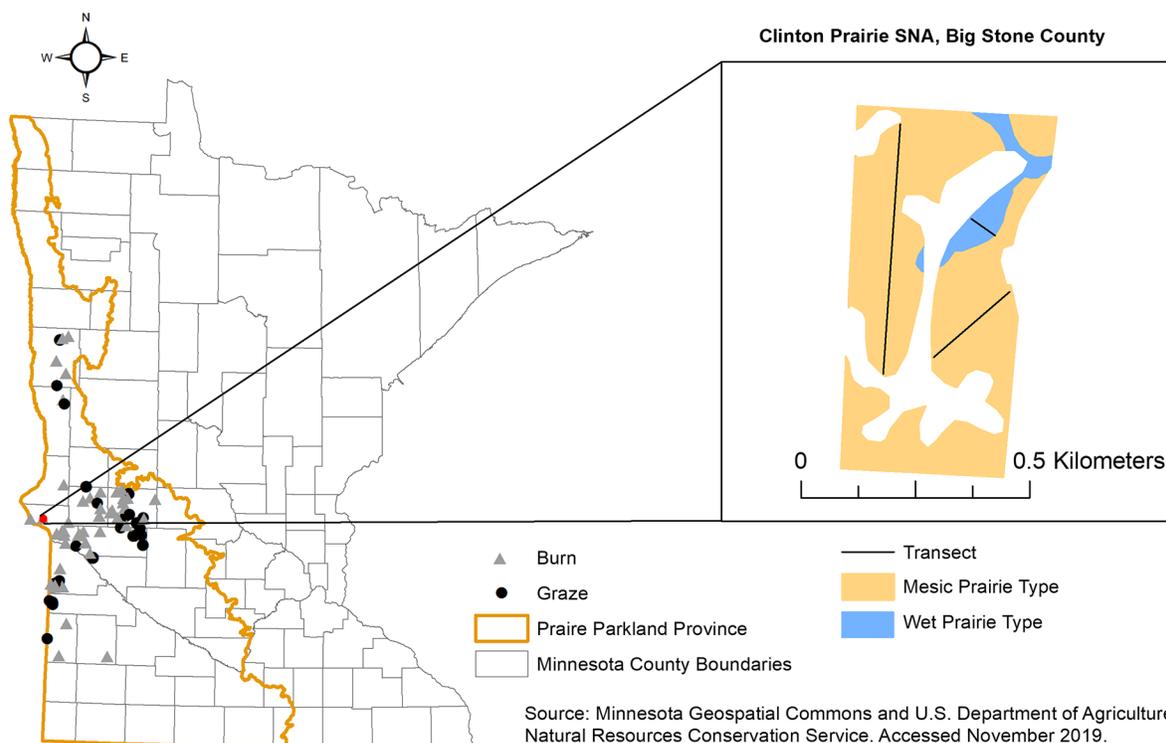


Fig. 1. Burned and grazed sites within the Prairie Parkland Province of Minnesota, USA. Expanded map indicates one site, which comprises mesic and wet prairie types, with randomly placed transects along which vegetation was measured and soil cores were collected.

Table 1. Number of sites (by prairie type) and the frequency (mean number of years/11 yr) and recency (mean number of years since management) of management for burned and grazed prairies.

Management	Prairie type	Sites (N)	Frequency of management	Recency of management
Burned	Dry	3	1.33	5.00
	Mesic	35	1.53	4.50
	Wet	30	1.48	4.39
Grazed	Dry	1	11.00	0.00
	Mesic	21	6.70	1.65
	Wet	16	6.75	1.25

calculated frequency ( $n$  occupied plots/total plots) by species for each prairie type in each site. In addition, a botanist-directed meandering walk through the site created a more complete species list for calculation of mean CofC of species present at the site.

### Soil sampling and analysis

Within each prairie type at each site, we collected and combined five, 10 cm deep  $\times$  2.54 cm diameter soil cores along a randomly selected vegetation transect to assess bulk density, soil texture, and potential nitrogen mineralization and nitrification. A second set of five, 10 cm deep  $\times$  2.54 cm diameter soil cores were collected along the same transect for total C and N. To determine bulk density, each composite sample of soil was weighed and a subsample removed to determine the oven-dry-to-air-dry ratio. Bulk density was calculated as the oven-dry weight of soil divided by its total volume. Texture analyses were performed at the Research Analytical Laboratory at the University of Minnesota (<http://ral.cfans.umn.edu/>) using the hydrometer method (Day 1965). Percent sand and percent clay results were then entered into the soil texture triangle (<http://resources.hwb.wales.gov.uk/VTC/env-sci/module2/soils/soilwatr>).

htm) to calculate field capacity ( $\text{cm}^3$  water/ $\text{cm}^3$  soil), the optimal moisture level for microbial activity (Barros et al. 1995); we used this information for subsequent laboratory incubations. Total C and N were measured at Carleton College, Northfield, MN. Samples were first finely ground on a mixer mill (CertiPrep 8000-D; SPEX SamplePrep, Metuchen, New Jersey, USA), and then, C and N concentrations were measured via combustion on an ECS 4010 elemental analyzer (Costech Analytical, Valencia, California, USA). Concentrations were converted to area-based values ( $\text{g}/\text{m}^2$ ) by multiplying %C or N by bulk density for each sample.

We performed laboratory incubations to determine potential net nitrification and mineralization rates. The entire soil sample from a given site was air-dried. One 5-g subsample was extracted with 2 mol/L KCl (methodology follows; Robertson et al. 1999) and is defined as the initial sample. A second 5-g subsample, also air-dried, was then brought to field capacity in a specimen cup and covered with a low-density polyethylene wrap (Glad brand cling wrap) to allow for gas exchange and minimize water loss and allowed to incubate for 28 d before extraction; this is the final sample. Following a 28-day incubation, the final sample was extracted with 2 mol/L KCl. The 2 mol/L KCl extracts were then analyzed by the University of Minnesota Research Analytical Laboratory for concentrations of ammonium ( $\text{NH}_4^+$ ) and nitrate/nitrite ( $\text{NO}_3^-/\text{NO}_2^-$ , hereafter referred to as nitrate; Henriksen and Selmer-Olsen 1970) using a Lachat QuikChem 8500 Flow Injection Analyzer. Mineralization rate ( $\mu\text{g}$  nitrogen  $\text{g}\cdot\text{soil}^{-1}\cdot\text{d}^{-1}$ ) is the sum of the initial ammonium and nitrate concentrations subtracted from the sum of the final ammonium and nitrate concentrations, divided by the incubation period of 28 d. Nitrification rate ( $\mu\text{g}$  nitrogen  $\text{g}\cdot\text{soil}^{-1}\cdot\text{d}^{-1}$ ) is the initial nitrate concentration subtracted from the final nitrate concentration, divided by the 28-day incubation period. These rates are an indication of N available for plant uptake.

#### Statistical analysis

We used nonmetric multidimensional scaling (NMS) in PCOrd v. 7.1 (McCune and Mefford 2016) to visualize overlap in plant communities, based on species' frequencies, on study sites

managed by fire and grazing and occurring on the three prairie types (dry, mesic, and wet). The distance measure was Bray-Curtis, and we ran 250 permutations each of observed and randomized data. Quantitative soil characteristics (percentage of sand, percentage of clay, nitrogen mineralization rate, and bulk density) and invasive plant species of interest were fitted as vectors on the graphs when  $r \geq 0.20$ . We obtained correlation coefficients of all plant species with the NMS axes to help interpret the ordination.

Because sites, and prairie types within sites, differed greatly in size (e.g., from 1.06 to 142 ha of wet prairie), we estimated plant species richness with rarefaction as implemented with the exact method (i.e., the expected species accumulation curve is determined by sample-based rarefaction; Chiarucci et al. 2008) in the `specaccum` function in `Vegan 2.5-4` (Oksanen et al. 2017) for R v. 3.4.2 (R Core Team 2015). Estimates were made for all species and, for only native species, encountered on plots. We used estimates for four plots as a basis for comparison among sites and prairie types to avoid measurements from extremely small prairie-type polygons dominated by edge. Thirteen of 119 prairie-type polygons within sites were too small to accommodate four plots and were excluded from comparisons of richness. Evaluation of plant species richness and Shannon evenness was based on data collected on plots on transects; data to evaluate CofC also included species found during the botanist-directed walk.

We used mixed-effects models (`proc mixed` in SAS v. 9.4; SAS Institute Inc. 2002–2012) to compare plant species richness, native plant species richness, Simpson's evenness, coefficient of conservatism (CofC; obtained from <https://universalfqa.org/> using the Dakotas 2017 database primarily and Iowa 2001 if the species was not found in the Dakotas database), frequency of the invasive grasses *Poa pratensis* and *Bromus inermis*, and soil properties (total N, total C, C:N, percentage of sand, percentage of silt, percentage of clay, net N mineralization, net N nitrification) between sites managed by fire or grazing. Models included management (burned or grazed), prairie type (dry, mesic, or wet), and their interaction as fixed effects and management nested within site as the random effect. Means with significant ( $P \leq 0.05$ ) treatment effects were separated with Fisher's

least significant difference, a method of post hoc pairwise comparison that retains the original experiment-wise error rate (Milliken and Johnson 2002). In addition, we used general linear models (proc glm in SAS v 9.4; SAS Institute, Cary, North Carolina, USA) to characterize mean CofC for plant species that were found exclusively in grazed or burned sites. Finally, we used Pearson correlation coefficients (proc corr in SAS v. 9.4; SAS Institute) to examine relationships between the number of times sites were managed over the 11-year period prior to sampling (hereafter frequency of management) and the number of years since management had occurred (hereafter recency of management), with vegetation variables species richness, native species richness, mean CofC, and frequencies of *B. inermis* and *P. pratensis*; and with soil variables bulk density, total N, total C, and net N mineralization and nitrification, on grazed and burned sites separately. We also examined correlations between stocking rate (AUM ac<sup>-1</sup>; a measure of grazing intensity) and these variables on grazed sites.

## RESULTS

Over two years of sampling, we recorded 399 plant species across all sites (328 on transects only); 59 were found only on burned sites, and 53 were found only on grazed sites (57 and 52 on burned and grazed sites, respectively, on transects only); 28% of all species recorded were exclusively found on either burned or grazed sites with the two most widespread exclusive species being the native *Grindelia squarrosa* on grazed sites and the non-native *Lactuca serriola* on burned sites (Appendix S1: Table S1). Fifty-eight species were recorded only once (52 on transects only). Twenty-two species were not in either of the databases we consulted for CofC, so were excluded from comparisons involving mean CofC. Sixty-seven species (approximately 17%), including observations on transects and botanist-directed walks, were non-native, with 53 species occurring on burned and 55 on grazed sites (Appendix S1: Table S1). Data are available at Larson et al. (2019).

A plot of the first two axes in the nonmetric multidimensional scaling (stress = 13.32 with 88 iterations for a 3-dimensional solution) illustrated that plant communities overlapped

broadly between sites managed with fire or grazing, but separation of wet and mesic prairie types was evident (Fig. 2). The first axis (representing 53% of the variation in the data matrix) was positively correlated with bulk density ( $r = 0.556$ ) as well as with a variety of species, the strongest correlations of which were with common cool- and warm-season grasses such as *Bouteloua curtipendula*, *Hesperostipa spartea*, *P. pratensis*, and *Schizachyrium scoparium* (Appendix S1: Table S1); the axis was negatively correlated with net N mineralization ( $r = -0.570$ ) and the invasives *Phalaris arundinacea* and *Cirsium arvense* (Appendix S1: Table S1; Fig. 2). Percent sand ( $r = 0.306$ ) and percent clay ( $r = -0.399$ ) also were very weakly associated with the first axis. Bulk density had a weak negative correlation ( $r = -0.388$ ) with the second axis (which represented 17% of the variation in the data matrix). The invasive grass, *B. inermis*, had a strong negative correlation with the second axis ( $r = -0.562$ ), and several native species associated with wetter soils (e.g., *Spartina pectinate*,  $r = 0.644$ ; *Zizia aurea*,  $r = 0.568$ ; and *Lathyrus palustris*,  $r = 0.543$ ) were positively correlated with the second axis (Appendix S1: Table S1). None of the soil variables, but several weedy species (e.g., *Agrostis gigantea*,  $r = -0.627$ ; *Elymus repens*,  $r = -0.484$ ; *Taraxacum officinale*,  $r = -0.458$ ) were negatively correlated with the third axis, which represented 16.4% of the variation in the data matrix.

Diversity metrics were not sensitive to management approach. Total species richness, native species richness, and Shannon's evenness did not vary with management (Fig. 3a–c) or prairie type, and there were no interactions between management and prairie type (Appendix S1: Table S2). Although both *P. pratensis* and *Bromus inermis* frequencies declined with increasing soil moisture (Fig. 4), neither was influenced by management type and there were no interactions between management and prairie type (Appendix S1: Table S2). Mean CofC did not vary between management types or among prairie types, nor did mean CofC vary between species exclusive to burned or grazed sites (Fig. 5).

Soil properties varied in their responsiveness to management approach. Bulk density was higher on grazed than burned prairies and declined with increasing moisture (Fig. 6), but there was no interaction between management

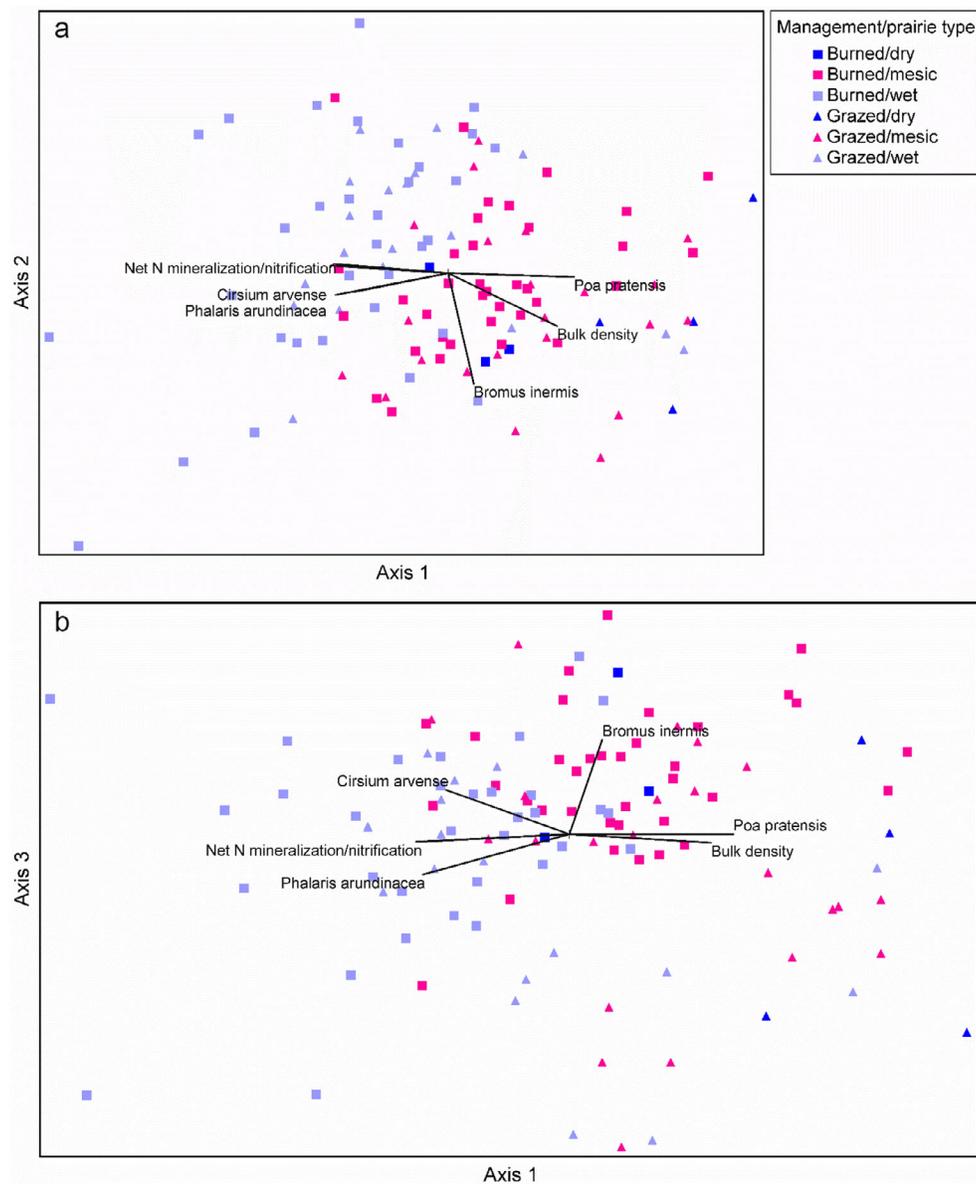


Fig. 2. Sites within species space for the nonmetric multidimensional scaling analysis of vegetation on grazed (circles) and burned (squares) sites (a, axes 1 and 2; b, axes 1 and 3). Dry (dark blue) and mesic (pink) prairie types tended to correlate with increasing soil bulk density and wet (lavender) prairie type with nitrogen mineralization rate. Vectors are proportional to the strength of the correlation with the axes. See Appendix S1: Table S1 for all correlations between species and NMS axes.

and prairie type (Appendix S1: Table S2). Total N was 22% greater on grazed than burned prairies (Fig. 7a) but did not vary with prairie type, and there was no interaction between management and prairie type. Total C did not

vary with management or prairie type, but C:N was 13% lower on grazed than burned prairies (Fig. 7b), apparently driven by differences in total N. Both net N mineralization and nitrification rates increased with increasing soil

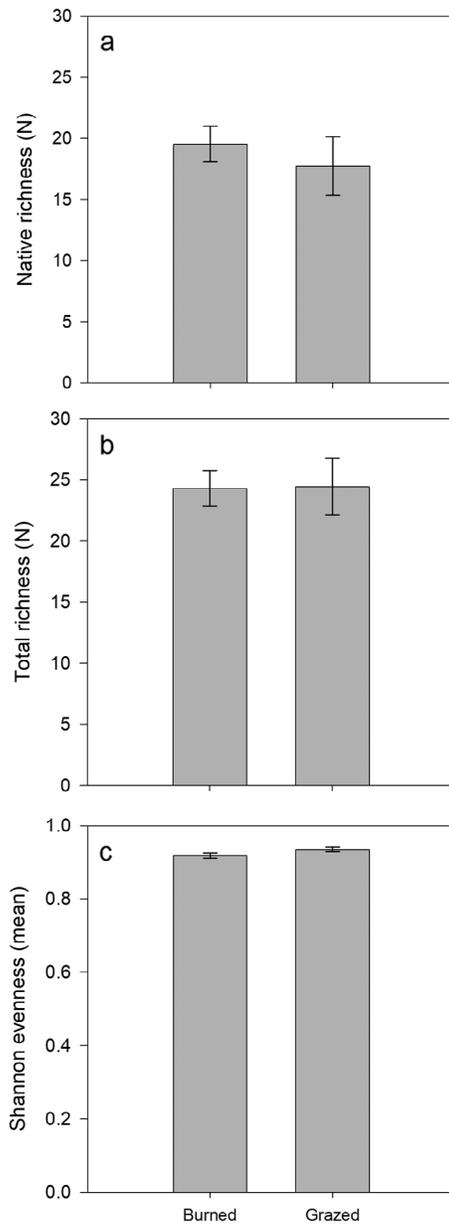


Fig. 3. Native (a) and total (b) species richness and Shannon's evenness (c) as a function of management approach. Shown are means  $\pm$  1 SE.

moisture (Fig. 8a, b) but were not influenced by management type, and there was no interaction between management and prairie type (Appendix S1: Table S2).

We found significant correlations for recency of management with measures of species

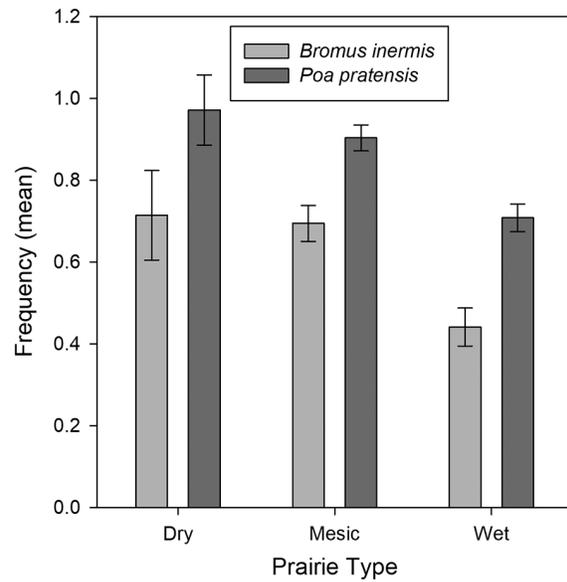


Fig. 4. Mean frequency of *Bromus inermis* and *Poa pratensis* in response to moisture regime of sampled prairies. Shown are means  $\pm$  1 SE.

richness and conservatism for burned but not grazed sites (Appendix S1: Table S3). Native and total species richness and mean CofC decreased with years since a site had been burned (Fig. 9a–c) but were unrelated to number of times the site had been burned over the 11-year period prior to sampling (Appendix S1: Table S3). Frequencies of *B. inermis* and *P. pratensis* were unrelated to burning frequency or recency, as were all the soil variables (Appendix S1: Table S3). In contrast, none of the species richness and conservatism measures were related to grazing frequency or recency, but all of the soil variables were; in each case, if the variable was positively correlated with grazing frequency, it was negatively correlated with recency and vice versa (Appendix S1: Table S3). *P. pratensis* increased with increasing frequency of grazing but declined with recency (Fig. 10a, b); the opposite was true for *B. inermis*, which decreased with grazing frequency and increased with the length of time since grazing had occurred (Fig. 10c, d). None of these correlations were strong. Neither maximum nor mean stocking rate was significantly correlated with any of the variables we measured (Appendix S1: Table S3).

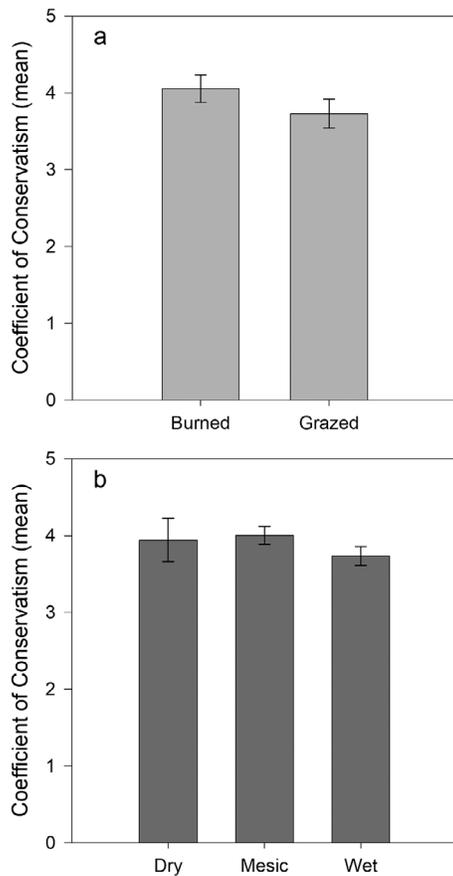


Fig. 5. Mean coefficient of conservatism in response to management approach (a) and moisture regime (b) of the sampled prairies. Shown are means  $\pm$  1 SE.

## DISCUSSION

In most respects, vegetation characteristics were similar when managed by grazing or by fire. Community composition overlapped broadly, species richness and evenness were similar, and mean conservatism of the species did not vary between the two management types nor between those species exclusive to one management type. That said, resource managers may find certain conservative species of interest to be favored by one or the other management types. For example, we found two hemiparasitic plants, *Castilleja sessiflora* and *Pedicularis canadensis*, only on burned sites; two species of milkweed, *Asclepias ovalifolia* and *A. tuberosa*, are hosts of monarch butterflies (*Danaus plexippus*) that we found

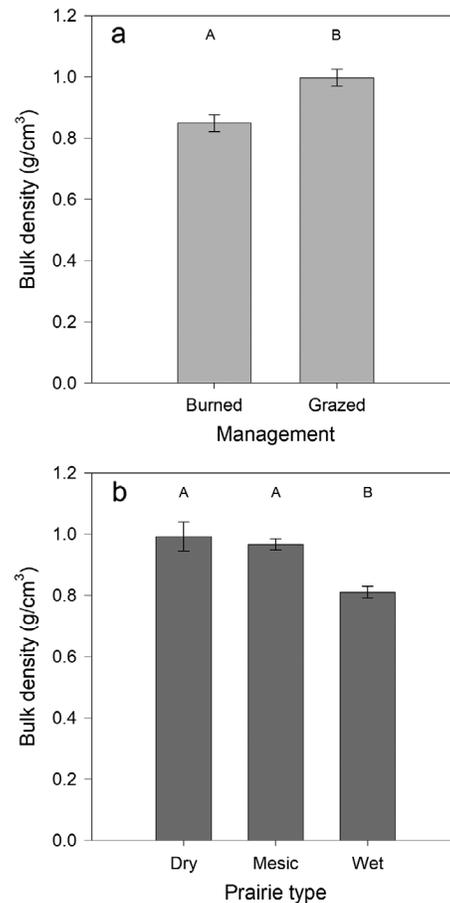


Fig. 6. Soil bulk density in response to management approach (a) and moisture regime (b) of the sampled prairies. Shown are means  $\pm$  1 SE. Different letters signify means that are significantly different from each other.

only on grazed sites. Despite > 25% of species in this study being found exclusively on either burned or grazed sites, the conservatism of the species, as measured by mean CofC, did not differ between the two management approaches. This suggests the importance of maintaining both fire and grazing by large ungulates on the prairie landscape. Neither approach was objectively better in our study, but both are needed to maximize prairie plant diversity.

Previous studies that compared prairies or grasslands managed by grazing and fire typically found greater species evenness on grazed sites due to selective grazing by either cattle or

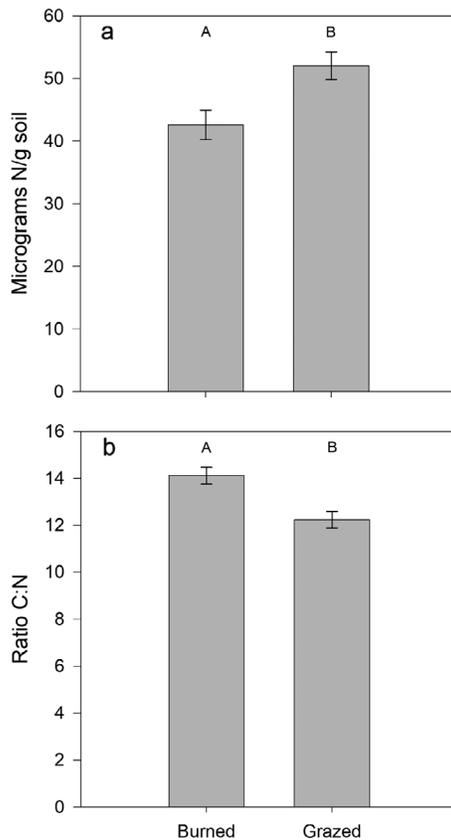


Fig. 7. Total N (a) and C:N ratio (b) in response to management approach. Shown are means  $\pm$  1 SE. Different letters signify means that are significantly different from each other.

bison that removed biomass of dominant grasses, thus allowing less competitive species to coexist (e.g., Elson and Hartnett 2017). Likewise, richness was greater at grazed than ungrazed prairies at Konza, regardless of fire frequency (Manning et al. 2017). The remnant prairies we studied had relatively high evenness, with the Shannon index ranging from 0.81 to 0.99; in contrast, Shannon-Weiner evenness at burned and unburned grazed sites studied by Eby et al. (2014) at Konza Prairie was all  $<0.8$ . Because our study was not experimental, we do not know species richness and evenness prior to application of fire or grazing. What is clear is that at least 11 yr of management by either fire or grazing resulted in comparably high evenness and no significant difference in richness between management approaches.

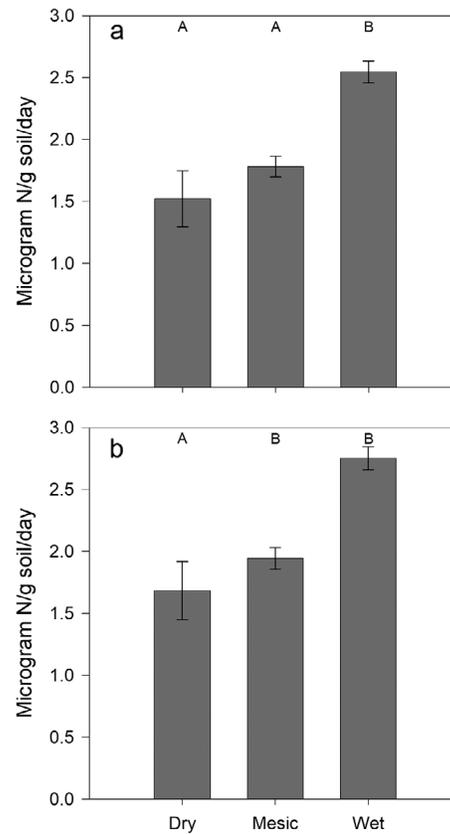


Fig. 8. Net N mineralization (a) and net N nitrification (b) rates in response to moisture regime at sampled prairies. Shown are means  $\pm$  1 SE. Different letters signify means that are significantly different from each other.

Invasive cool-season grasses are a major threat to both remnant and reconstructed prairies in the midwestern United States (DeKeyser et al. 2015, Larson et al. 2017). DeKeyser et al. (2013) suggested that cessation of disturbance contributed to invasion at study sites near the Missouri River in North Dakota. Frequencies of *B. inermis* and *P. pratensis* did not vary between fire and grazing management in our study, and we only observed correlations with frequency and recency of management with grazing, not fire. In agreement with Biondini et al. (1998), *P. pratensis* was positively associated with grazing frequency, suggesting tolerance to grazing. In contrast, *B. inermis* was negatively associated with grazing frequency. As these two species often co-occur, it may be difficult to manage them with grazing

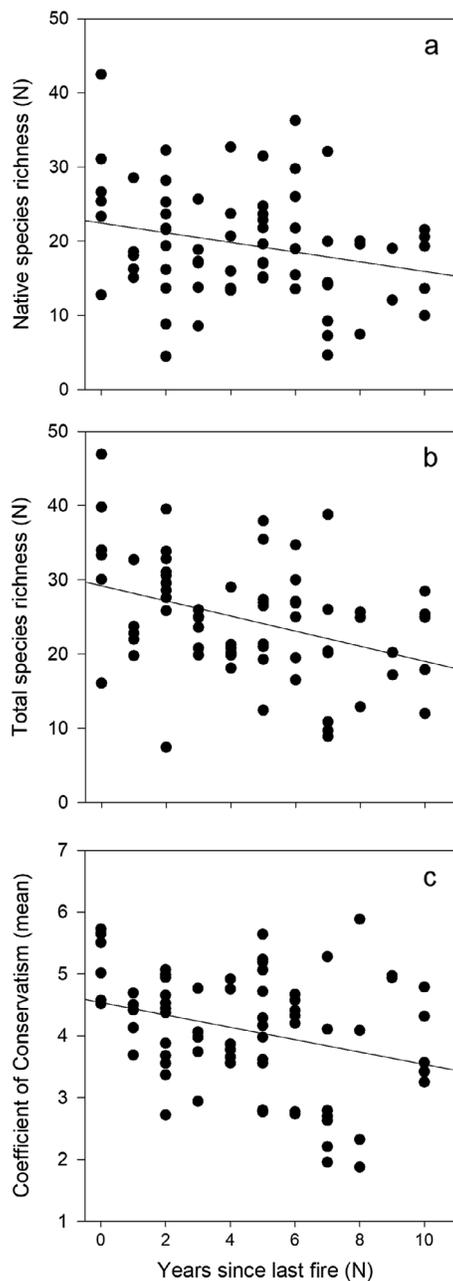


Fig. 9. Native (a) and total (b) species richness and mean coefficient of conservatism (c) at sites managed by burning as a function of recency of fire (years since last fire).

alone, but we observed no correlations with fire frequency to suggest this as an alternative management technique. The relatively infrequent application of fire at our study sites may reduce

its effectiveness, however. Willson and Stubben-dieck (1997) found that carefully timed and repeated fire could control *B. inermis* in Nebraska, suggesting the need for more consistently applied fire than was the norm in our study sites.

Compared to management frequencies at Konza Prairie, where, for example, some units have been burned every year for decades (Manning et al. 2017), our burned sites received relatively light disturbance. Many sites had been burned only once and only one prairie was burned four times in the 11 yr leading up to this study, yet time since fire was significantly negatively correlated with total and native species richness and conservatism. A similar relationship between burning and mean CofC (but not species richness) was found in reconstructed prairies in Minnesota (Larson et al. 2018), suggesting the potency of fire to affect species composition in these northern tallgrass prairies. Similarly, fire frequency and mean CofC were correlated in the southern prairies at Konza, although species richness was not (Manning et al. 2017). Sites managed by grazing in our study saw a broader range of disturbance frequency in the 11 yr prior to sampling than those managed by fire, with none of the sites grazed less than twice, but 10 sites that were grazed every year. Nonetheless, we did not detect any relationship between grazing frequency or recency and plant species richness or conservatism.

Soil properties were minimally affected by management treatments, with only bulk density and total N increased under grazing. Higher bulk density under grazing is common due to soil compaction, but the response of total soil N is highly variable across studies (Milchunas and Lauenroth 1993, Byrnes et al. 2018). It is expected that rates of N cycling (i.e., rates of N mineralization and nitrification) also would be higher under grazing, as cattle reduce aboveground C inputs, consume plant N, and release it as waste in more labile forms (Johnson and Matchett 2001). However, microbial activity may be more sensitive to variation in grazing intensity within a single stocking rate, as grazing is not uniform within a grazing treatment (Esch et al. 2013). While we observed no effect of management type on N cycling, rates of mineralization and nitrification were both responsive to soil moisture,

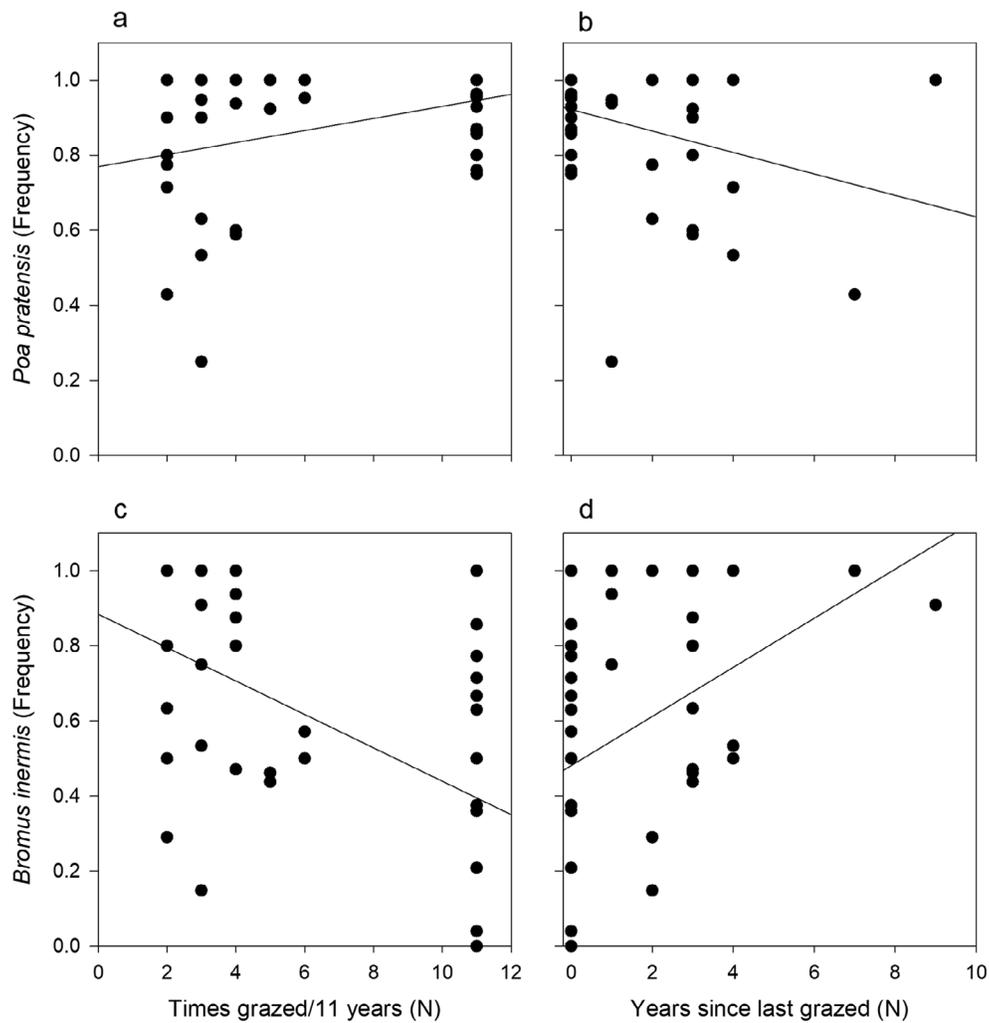


Fig. 10. Frequency of *Poa pratensis* as a function of grazing frequency (a) and recency (b) and of *Bromus inermis* as a function of grazing frequency (c) and recency (d).

suggesting that rates of N cycling were perhaps more dependent on water availability than C limitation and N availability in these prairies. There was also no effect of management or prairie type on total soil C. This is in contrast to previous studies that have found that continuous grazing reduces soil organic C compared to ungrazed sites, although this effect is strongest under heavy grazing regimes (Byrnes et al. 2018). Our results suggest that for the range of grazing intensity (0.99–7.19 AUM/ha) in the remnant prairies we studied, grazing does not reduce soil C content when compared to management by burning. Grazing intensity at our sites was

slightly higher than the 0.67–3.66 AUM/ha (0.27–1.48 AUM/ac; <https://efotg.sc.egov.usda.gov/>) recommended grazing intensity to achieve 25% harvest efficiency (50% utilization) in similar soils in South Dakota; no technical guidance is available for Minnesota.

As noted in our methods, this study was observational. We did not randomly apply treatments to sites and cannot know how the variables we measured differed prior to application of treatments. If certain site characteristics were more likely to suggest a site be managed in a particular way, the outcome of this study could be biased. Likewise, our understanding of the

environmental conditions prior to and immediately following treatment applications is limited due to imprecise and inconsistent record-keeping. Nonetheless, evidence suggests that our study sites were in general comparable. For example, soil texture would remain constant regardless of management and would likely be associated with any preference in how the site was managed, yet soil texture did not vary systematically between our burned and grazed sites (Appendix S1: Fig. S1). Similarly, the distributions of prairie types were similar in burned and grazed sites (Table 1) and we found no interactions between management approach and prairie type for any of our response variables. Thus, although an experimental approach is desirable and feasible in some circumstances (e.g., LTER sites), documenting outcomes on existing working landscapes also has value and can provide direction to land managers (e.g., Roche et al. 2014).

## CONCLUSION/MANAGEMENT CONSIDERATIONS

The hypothesis that the two approaches to tallgrass prairie management, fire and grazing, would produce different plant community and soil characteristics was only partially supported. Soil bulk density and total N (and therefore C:N) varied significantly with management approach, but from a plant community perspective, the 28% of species that were exclusively found in one or the other of the management types suggest the need for considering the broader landscape when designing management plans. Relying on only one of these management approaches will reduce overall plant species richness across the landscape. Where invasion by *P. pratensis* is observed to be the greatest threat, however, fire may ultimately be a better management tool, since the species is highly tolerant of grazing. If resources allow, more precise timing of fire may reduce *B. inermis* (Willson and Stubbendieck 1997) and simultaneously not favor *P. pratensis*. Our results also show that the impact of fire declines with time, so increasing fire frequency to 3–4 fires/decade on highly valued prairies may be a reasonable management goal.

The lack of correlation between frequency or recency of grazing, or of stocking rates, and species richness or mean CofC suggests that the

levels of grazing intensity we monitored in these tallgrass prairie remnants may be consistent with conservation grazing (Asensio and Lauenroth 2012). Effects of management by grazing vs. fire in midwestern tallgrass prairies may diverge if grazing is applied more intensively, however (Byrnes et al. 2018). Globally, C stocks have been found to decline and bulk density to increase with high grazing pressure (Abdalla et al. 2018). Over time, such changes in soils can be expected to affect plant community composition.

## ACKNOWLEDGMENTS

We are indebted to the field crews who collected data each year: Karin Jokela, Kathryn Schmidt, Larissa Mottl, and Madison Rancour. Aaron Schwab contributed to the soil C and N analysis. Deborah Buhl provided statistical advice during all phases of the study. We are grateful to Marissa Ahlering and two anonymous reviewers who provided valuable comments on an earlier version of the manuscript. We thank the land managers and private landowners who allowed us access to their property to conduct surveys. Funding for the study was provided via a grant from the Minnesota Environmental and Natural Resources Trust Fund and from U.S. Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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