

Bison Grazing in Eastern Tallgrass Prairie Does Not Alter Plant Diversity after Five Years

Authors: Chakravorty, Jennifer, Harrington, John A., and Bach,

Elizabeth M.

Source: Natural Areas Journal, 44(4): 215-222

Published By: Natural Areas Association

URL: https://doi.org/10.3375/2162-4399-44.4.215

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Bison Grazing in Eastern Tallgrass Prairie Does Not Alter Plant Diversity after Five Years

Jennifer Chakravorty, 1 John A. Harrington, 1 and Elizabeth M. Bach^{2,3}

¹University of Wisconsin-Madison, College of Letters and Sciences

³Corresponding author: elizabeth.bach@tnc.org; 515-509-0297

Associate Editor: Young D. Choi

ABSTRACT

North American tallgrass prairie evolved with regular fire set by Indigenous people and grazing from large herbivores, including the plains bison (*Bison bison*). In contrast to uniform effects of prescribed fire, bison graze selectively, creating increased heterogeneity on the landscape. We examined plant community responses to reintroduced bison grazing in high-diversity native and restored tallgrass prairie in Illinois, USA. We evaluated plant community diversity and structure in paired grazed and ungrazed (fenced) plots. After 5 y of grazing at a relatively low target stocking rate of 1 animal unit per 5.2 ha (13 acres), there were no differences in plant community diversity, composition, nonnative:native species ratio, or visual obstruction readings between grazed and ungrazed plots. An interaction exists (or was found) between plant community type and grazing in which grazed savanna plots had greater grass relative abundance compared to ungrazed plots. Ongoing monitoring will evaluate long-term trends.

Index terms: bison; diversity; grazing; plants; tallgrass prairie

INTRODUCTION

The prairie, once the largest ecosystem in North America, covering about 15% of the continent, created a triangle that spanned from Saskatchewan and Manitoba in Canada, west to the foothills of the Rocky Mountains, south into Texas, and east into Indiana (Robertson et al. 1997; Anderson 2006). Of the original ~69 million ha of prairie once found across the United States, ~9 million ha occurred in what is now the state of Illinois (Corbett 2004). As of 2018, only 1010 ha of high-quality prairie remains in Illinois, with most less than 5 ha in size (Corbett 2004). Conversion of land to agricultural uses followed by fire suppression are common reasons for prairie loss (Anderson 1970). With this extreme loss of the prairie ecosystem, establishment and proper management of restorations and prairie remnants is particularly valuable.

Prairie, especially eastern tallgrass prairie which typically receives >800 mm of precipitation each year, is a disturbance-dependent ecosystem. Historically, this grassland ecosystem relied on both fire and grazing disturbances for its existence (Knapp et al. 1999; Collins 2000; Fuhlendorf and Engle 2004). Prior to European settlement, Native Americans were key in maintaining the grass-dominated vegetation of the North American prairie (Curtis 1959; Anderson 1990, 2006). This relationship between Native Americans and the burning of grasslands extends back 30,000 y (Bragg 1995) and was used to prevent woody encroachment of grasslands, increase hunting access, encourage prairie growth, clear areas for agriculture, control insects, and ease traveling (Stewart 1956; Curtis 1959; Pyne 1982; Anderson 2006).

The prevalence of bison on the grasslands of North America has dramatically changed over the past 200 y. Rampant hunting from 1830 to 1880 reduced the estimated number of bison from 30–60 million (Shaw 1995) to a few thousand (Knapp et al. 1999). Therefore, our understanding of the extent of a freerange bison's influence on the tallgrass prairie is limited (McHugh 1972; Flores 1991). Bison restricted in range to large properties demonstrate a diet preference largely composed of grasses, preferably the warm-season prairie grasses, and sedges with less than 10% consumption of woody vegetation and forbs (Knapp et al. 1999). Based on documentation of large numbers of bison east of the Mississippi by French explorers and Jesuit missionaries, researchers estimate that maximal bison populations were found in the prairie peninsula of Illinois during the 17th and 18th centuries (Bamforth 1987; McMillan 2006)

Without fire and grazing, the accumulation of plant litter and dominance of grass reduces forb abundance and diversity, the latter a key element contributing to the diversity of prairies (Collins 1992; Briggs and Knapp 1995; Fuhlendorf et al. 2009). While burning in grasslands favors a homogeneity of dominant grasses and a reduction in woody vegetation, bison grazing reduces grass density and competition thereby increasing forb abundance and diversity (Hartnett et al. 1996; Collins et al. 1998; Knapp et al. 1999; Powell 2006). Fuhlendorf and Engle (2004) stress that, although the effects of bison and fire are often studied individually, the interaction between these disturbances is more important than the sum of either individual effect. Importantly, bison prefer to graze in recently burned areas, regardless of fire season (Knapp et al. 1999; Fuhlendorf and

²The Nature Conservancy – Nachusa Grasslands, 8772 S. Lowden Rd., Franklin Grove, IL 61031

Engle 2004; Vermeire et al. 2004; Allred et al. 2011; Winter et al. 2015). This preference has far-reaching effects for ecosystem processes in the landscape (Archibald et al. 2005; Fuhlendorf et al. 2006; Leonard et al. 2010; Allred et al. 2011). The dominant grasses are suppressed, forbs and bare ground increase, and without fuel, fire is unlikely. Where bison did not graze litter accumulates and these are the patches likely to burn during fire activity. Once burned again, bison return to graze and a shifting patch pattern of burned, grazed, and untouched units occurs (Biondini et al. 1999; Fuhlendorf and Engle 2004). These feedbacks create a "shifting mosaic" and increase the degree of temporal and spatial heterogeneity across the landscape (Hartnett et al. 1996; Knapp et al. 1999; Fuhlendorf and Engle 2004; Powell 2006; Blackburn et al. 2020).

This spatial heterogeneity is challenging to replicate with restored tallgrass prairie, which are often small (tens to hundreds of acres) and in a landscape context of row-crop agriculture. Decades of restoration efforts have gained success in re-establishing native vegetation; however, over time these plantings often became dominated with warm-season native grasses (Grman et al. 2013). While prairies are grass-dominant, many of these plantings were lacking in the flowering plant diversity observed in unplowed native prairies, even with frequent burning. With accruing evidence that bison grazing was a fundamental ecological factor for tallgrass prairie, managers began hypothesizing how reintroducing grazing may sustain plant (and animal) diversity on restored prairies. A handful of restored prairie sites are large enough to accommodate bison reintroduction. Bison have strong matriarchal herd social dynamics across generations (King et al. 2019) and require at least modest-sized herds and large contiguous landscapes for grazing. In addition to numerous intact native prairies, a few larger tallgrass prairie restorations have reintroduced bison, including the Neal Smith National Wildlife Refuge (US Fish and Wildlife Service, Iowa) and Dunn Ranch Preserve (The Nature Conservancy, Missouri). Where introduced, grazing coupled with seed additions have been observed to maintain or increase plant diversity in restored tallgrass prairie (Wilsey and Martin 2015).

In October of 2014, one of the first conservation herds of bison east of the Mississippi River was introduced to The Nature Conservancy's Nachusa Grasslands (hereinafter, Nachusa) to increase plant diversity and heterogeneity. Although bison were historically present in this area of Illinois, The Nature Conservancy's decision to reintroduce bison at Nachusa was first and foremost based in land management rather than simple replication of historical free-ranging bison herds once found in the region. Expectations from land managers include reduced warm-season tallgrass abundance, increased forb abundance and diversity, and niche space for plants and animals that need more open structure (Kleiman 2016). In this study, we ask what effect 5 y of bison grazing has on the plant community at Nachusa. We investigated plant species diversity, composition, abundance, and visual obstruction readings (VOR) in paired grazed and ungrazed plots, including baseline measurements prior to bison reintroduction. Our hypotheses were as follows: (1) As

compared to burned plots without grazing, plots with grazing and burning have increased species diversity, greater proportion of forb to grass abundance, and greater proportion of native to nonnative species. (2) VOR are lower in grazed plots compared to ungrazed plots.

METHODS

Nachusa Grasslands is located near Franklin Grove, Illinois (41.883706°N, -89.342410°W) and is owned and managed by The Nature Conservancy (TNC). Nachusa consists of more than 1600 ha of native prairie remnants, restored prairies, savannas and woodlands, and wetlands. More than 700 native plant species and 180 breeding or migrating bird species have been identified on the site. Precipitation averages 675 mm during the growing season (1 April–30 September) and 1030 mm annually. Average annual temperature from 1991 to 2020 was 9.6°C, with an average minimum and maximum temperature of 4.5°C and 14.8°C, respectively (U.S. Climate Normals; NCEI 2022).

In 2014, American bison (*Bison bison*) were reintroduced to Nachusa in a phased approach. An initial 30 animals were released onto \sim 200 ha (the north unit) in fall 2014 and grazed exclusively in the north unit for the 2015 growing season. In addition to 20 calves born in spring 2015, an additional 20 adult animals joined the herd in fall 2015 and the grazing area was expanded to include the 400 ha south unit. Since winter 2015/16, the herd has had full access to the entire 600 ha grazing area. After 2018, the herd has been managed at approximately 100 adult animals.

To examine the impact of bison grazing on plant communities, twenty-two 10 m × 18 m fenced plots (exclosures) and paired unfenced plots were established prior to bison reintroduction (Fig. 1). Fences are electrified metal wire. The plots are stratified to represent the habitat types at Nachusa (Table 1). There are six sampling sites on native prairie (n = 3in the north unit, n = 3 in the south unit), six sampling sites on older plantings (n = 3 in the north unit, n = 3 in the south unit), four sampling sites on newer plantings (n = 3 in the north unit, n = 1 in the south unit), and three sampling sites on savannas (n = 3 in the south unit). There are three additional sampling sites on wetlands in the south unit, which were not included in the analyses presented here due to the substantially different plant community. This unbalanced design results from uneven representation of these habitat types across the preserve. For example, there are no savanna or wetland habitats in the north bison unit. The stratified experimental design ensures three independent replications of each habitat type, and where possible more than three. All treatment areas but one were included in areas that had been burned within 2 y of sampling.

We used a stratified random approach to placing exclosures on the landscape within each habitat type. Habitat types are not randomly distributed across the site, which constrained a true random placement of sampling sites. Some habitat types only encompass small patches (1–2 ha) within the landscape and exclosures were placed where adequate space was available. Native prairie and wetland habitats at Nachusa primarily exist in

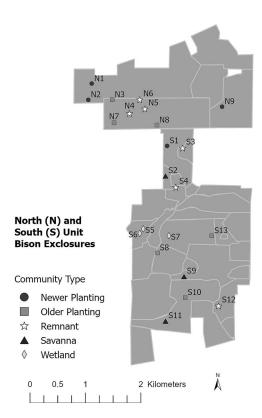


Figure 1.—Location and habitat type of exclosures at Nachusa Grasslands.

patches <5 ha. For each exclosure, three 12.5 m permanent transects inside the fence (ungrazed) are paired with three transects of the same length outside the fence (grazed) (Supplemental Fig. S1). Transect lines are located at least 2 m from fence lines and each transect is 3 m from the adjacent transect. Quarter-square-meter quadrats are placed on the east side of each transect line at five regular intervals (0–0.5 m, 3–3.5 m, 6–6.5 m, 9–9.5 m, and 12–12.5 m) for a total of 15 quadrats in each grazed and ungrazed plot.

Species Diversity, Abundance, and Composition

Within each 0.25 m² quadrat, we identified all species rooted in the sub-plot and visually estimated their percent cover for a total of 570 surveyed quadrats. Plots were sampled regardless of whether they had been grazed recently. Plant nomenclature follows Wilhelm and Rericha (2017). Plant community composition and cover were determined in the north unit in 2014 (pre-bison), 2017, and 2019. In the south unit, data were collected in 2015 (pre-bison), 2018, and 2020. Because the bison were introduced to the north unit in fall 2014 and the south unit in fall 2015, this corresponds to year zero, three, and five for each grazing unit. In 2014, Daubenmire cover classes (Daubenmire 1959) were used instead of percent cover. Class 1 is 0-5% coverage, class 2 is 5-25%, class 3 is 25-50%, class 4 is 50–75%, class 5 is 75–95%, and class 6 is 95–100%. To include the 2014 data in our analyses, we converted the 2015-2020 data to Daubenmire classes and then transposed all data to percent cover midpoints. For this analysis, all plants in the *Poa* genus

Table 1.—Surveyed exclosure plots and their habitat type, when the units were restored, years since last burned, and burn season. "N" denotes that the plots were in the north bison unit and "S" denotes that plots were in the south bison unit. *Wetland plots were not included in our analyses.

Site ID	Habitat Type	Year Restored	Years Since Last Burned (for survey years 2019 & 2020)	Burn Season
N1	Newer Planting	2009	0	Spring
N2	Newer Planting	2008	1	Spring
N9	Newer Planting	2011	0	Spring
S1	Newer Planting	2012	1	Spring
N3	Older Planting	2000	1	Spring
N7	Older Planting	2001	1	Spring
N8	Older Planting	2001	1	Spring
S8	Older Planting	1988	1	Spring
S10	Older Planting	1985	1	Spring
S13	Older Planting	1992	1	Spring
N4	Native Prairie	_	1	Spring
N5	Native Prairie	_	1	Spring
N6	Native Prairie	_	1	Spring
S3	Native Prairie	_	6	Spring
S4	Native Prairie	_	1	Spring
S12	Native Prairie	_	2	Spring
S2	Savanna	_	1	Spring
S9	Savanna	_	2	Spring
S11	Savanna	_	1	Spring
S7*	Wetland, Older Planting	1992	1	Spring
S5*	Wetland, Native	_	1	Spring
S6*	Wetland, Native	_	1	Spring

were converted to *Poa* spp. and all plants in the *Carex* genus were converted to *Carex* spp.

Aboveground Visual Obstruction Readings

In 2019 and 2020, aboveground plant visual obstruction readings (VOR) were recorded near the time of peak biomass (late August) in each plot using a Robel pole (Robel et al. 1970; Benkobi et al. 2000). VOR is used as a rapid method to estimate vertical cover or standing biomass and vegetation structure (Smith 2008; USDA USFS 2009). Robel poles have alternating bands of color every 10 cm on a pole, starting with zero at the bottom. The Robel pole was placed at two points along the center transect in each grazed and ungrazed plot. The lowest height band of the pole completely visible was recorded, and measurements were taken from 4 m in each direction from the pole (North, South, East, West). The four measurements were averaged for each grazed and ungrazed plot. Generally, higher VOR is correlated with more aboveground biomass (Joubert et al. 2015).

Data Analysis

All analyses were performed in RStudio (R Core Team 2020; RStudio Team 2020). Differences in the Shannon-Weiner Diversity Index (H'), average percent cover of grasses to forbs and nonnative to native species, and VOR (2019/2020 plot surveys) were tested using linear mixed-effects models in the *nlme* package (*lme* function) (Lokonon et al. 2019; Pinheiro et al. 2020). The Shapiro-Wilk test was used to assess normality of the data and the Levene's test was used to test for equal

variance of the data (Schultz 1985; Yazici and Yolacan 2007). To meet required model assumptions of normality, transformations included the natural log of the ratio of grasses to forbs, the inverse ratio of nonnative to native species, and the natural log of VOR. Fixed factors included habitat type (restorations, remnants, savannas), years since bison were introduced, and grazing treatment (grazed or ungrazed). Prescribed fire was included as a random effect. In some cases, habitat type could also be considered a random factor, but in this experiment, sampling sites were intentionally placed across community types in a stratified random design, making it a fixed factor. We evaluated AIC scores for full (including all interactions), partial, and main (no interactions) models. For all response ratios, the main model had the lowest AIC value, and no interaction terms were statistically significant, we analyzed all data with the main model. The one exception was a statistically significant interaction between graze and year since bison for the non-native:native plant ratio, which we retained in that model. Because differences between new and old restorations were not pronounced, restorations were combined into one community category to increase the sample size for statistical analyses.

We graphed dissimilarities between plant community species composition using nonmetric multidimensional scaling (NMDS) (Prentice 1977). Differences in species composition and functional group composition were further tested for using PERMANOVA in the vegan package in R (adonis function, Bray-Curtis dissimilarity matrix) (Anderson and Walsh 2013; Oksanen et al. 2020). Community type, year surveyed, grazing treatment, and the interaction between these were used as fixed factors. Post hoc analyses included PERMANOVA models constrained by habitat type or years since bison introduction. We carried out a secondary regression analysis to understand whether years since burning had an impact as a covariate using the vegan package in R (envfit function) (Dixon 2003; Oksanen et al. 2020). Prescribed fire is a regular management practice at Nachusa and time since last fire was consistently ≤ 2 y across all habitats. All code is openly accessible through GitHub repository Nachusa_BisonGraze5 (https://github.com/ebach/Nachusa_ BisonGraze5; permanent and citable DOI will be issued after article acceptance).

RESULTS

Plant community diversity, nonnative:native species ratio, grass:forb ratio, and VOR did not differ between grazed and ungrazed plots overall. There was an interaction with community type in which grazed plots in savannas had higher grass:forb ratios. This difference was consistent across all sampling years, indicating these differences were present before bison were reintroduced ($F_{3,100} = 4.77$, P = 0.004; Supplemental Fig. S2). Native prairies and older restorations had greater plant Shannon's diversity ($F_{3,103} = 45.54$, P < 0.0001) and grass:forb ratio ($F_{3,100} = 17.81$, P < 0.0001) and lower nonnative:native plant ratio (outlier removed, $F_{3,85} = 4.12$, P = 0.009) compared to savannas and new restorations (Fig. 2). VOR was only

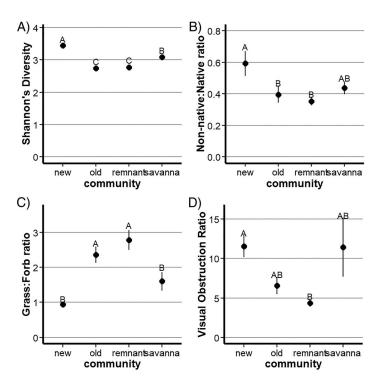


Figure 2.—Plant community Shannon's diversity (A), P < 0.01), non-native:native plant ratio (B), P = 0.01), grass:forb ratio (C), P < 0.01), and visual obstruction ratio (D), P = 0.02) all varied among the habitat types. Points represent mean values. Error bars are ± 1 standard error.

collected in year five after bison. Native prairies had the lowest VORs ($F_{1,30} = 3.97$, P = 0.02; Fig. 2), likely reflecting that native prairies on this landscape are all located on the top of dry sandy hills, which limit plant growth. New restorations had the highest VORs, which may reflect more mesic conditions and/or the low grass:forb ratio.

Year since bison reintroduction impacted Shannon's diversity and grass:forb ratio. Shannon's diversity was greatest 5 y after bison reintroduction ($F_{2,103} = 7.84$, P = 0.0007; Fig. 3). Grass: forb ratio was lowest 3 y after bison reintroduction ($F_{2,100} = 6.51$, P = 0.004; Fig. 3). Year three sampling was done in 2017 and 2018; both years had above average precipitation during the growing season. Nonnative:native plant ratio was the only response variable to exhibit an interaction. There were no differences in nonnative:native plant ratio in years zero and three; however, in year five, grazed plots had a greater nonnative:native plant ratio than ungrazed plots ($F_{2,100} = 3.84$, P = 0.03; Fig. 3). Analysis within habitat types showed no differences between grazed and ungrazed plots.

Plant community composition was distinct among all prairie habitat types (PERMANOVA, P = 0.001, $R^2 = 0.276$; Fig. 4). Time since burn was correlated with overall plant community composition (P = 0.05, $R^2 = 0.07$), but only accounting for 7% of differences. Numerous species were distinct indicator species for the three prairie types (Supplemental Table S1) including dominant warm-season tallgrasses (Sorghastrum nutans, Andropogon gerardii) in older plantings and native cool-season grasses in remnants (Dichathelium spp., Hesperostipa spartea).

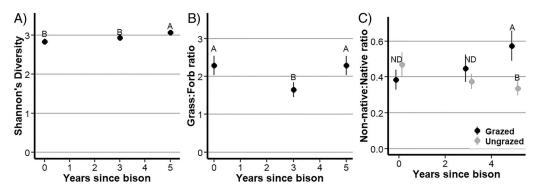


Figure 3.—Shannon's plant diversity (A) was greatest in year five (P < 0.01). Grass:forb ratio (B) was lowest in year three (P < 0.01). (C) The ratio of non-native:native plants exhibited an interaction between year since bison were introduced and grazing status (P = 0.03). In year five, grazed plots (black) had greater non-native:native plant ratios than ungrazed plots (gray). Points represent mean values. Error bars represent ± 1 standard error.

Savanna habitats had the greatest variation in composition and did not differ from old restorations or native prairies. Unsurprisingly, savanna habitats were distinguished by several species of trees (*Quercus* spp., *Celtis occidentalis, Ulmus americana*), vines (*Toxicodendron radicans, Vitis vulpine*), and shrubs (*Rubus* spp.) (Supplemental Table S1). In addition, community composition varied in year five after bison reintroduction compared to year zero baseline (P = 0.031, $R^2 = 0.020$; Supplemental Fig. S3). These differences were present in both grazed and ungrazed plots. This difference was in part driven by greater variability in plant community.

DISCUSSION

The results of this study imply that in the first 5 y, bison have had minimal, if any, effects on the vegetation diversity, composition, abundance, and structure at Nachusa Grasslands. Plant communities were distinct across community types, as expected. Across the 5 y, there were some modest changes in plant communities, which were consistent between grazed and ungrazed plots. The one important exception being a greater nonnative:native plant species ratio in grazed plots in year five. These results match those reached by Blackburn et al. (2020) who compared sites within the bison grazing area with sites outside the bison grazing area after the first 3 y of bison reintroduction at Nachusa. These consistent findings using

independent experimental designs indicate that bison have had a limited effect on vegetation change at Nachusa since their introduction.

Comparison with Other Bison Reintroduction

Previous studies in the western edge of the tallgrass prairie have shown that bison grazing reduces grass density and competition leading to an increase in forb abundance and diversity (Hartnett et al. 1996; Collins et al. 1998; Knapp et al. 1999; Powell 2006). Impacts on forb and grass abundance were observable at Konza Prairie Biological Station after 6 y with bison stocking rates like Nachusa. In contrast, this study found no change in plant diversity or grazing-correlated changes in grass cover or grass:forb ratio. Explanations may be that at the current stocking rate bison are not impacting grasses and that grasses are benefitting from fire, that the bison have not been on site for sufficient time to have any impact, or that if impact is occurring the sampling design is inadequate to capture it. Baseline plant diversity at Nachusa was greater and contained greater forb cover than baseline measures observed at Konza Prairie. There is likely an upper limit on plant diversity, and it is possible Nachusa diversity baseline is/was closer to this limit. In contrast, Konza Prairie exists in a landscape of intact and historically grazed native grasslands, providing a potential regional native seed source. Nachusa exists in a landscape of

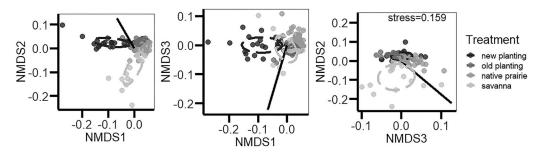


Figure 4.—A three-dimensional non-metric multidimensional scaling (NMDS) ordination visualizes differences in plant community composition among new and old prairie plantings, native prairie, and savanna habitats at Nachusa Grasslands (PERMANOVA P < 0.01). Solid black line shows the correlation of time since last prescribed fire (P = 0.05, $R^2 = 0.07$).

row-crop agriculture and passive recruitment of native seed is less likely.

The marginal trend of higher average proportion of nonnative to native percent cover in grazed plots in 2019 and 2020 is worth continued monitoring. Bison are known dispersers of graminoid and forb seeds (Rosas et al. 2008) and can introduce nonnative species while moving throughout the bison enclosure on their hair or in dung (Constible et al. 2005; Rosas et al. 2008). In addition, increased bare ground because of trampling and wallowing behaviors (Grudzinski et al. 2016) may be creating germination opportunities. If bison are dispersing seeds of nonnative species, their increased management within the bison unit may be necessary.

Additionally, average VOR were lower in grazed plots for all community types. Bison are important for grassland management because their preferential consumption of dominant grasses results in an overall reduction of aboveground biomass for grassland communities (Knapp et al. 1999). A lower VOR indicates aboveground biomass has been reduced in the grazed plots compared to ungrazed plots. Removal of biomass often results in greater heterogeneity across the landscape (Vinton et al. 1993; Coppedge and Shaw 1998), and increased heterogeneity is beneficial to meeting the needs of a greater variety of fauna (Powell 2006). For example, while declining grassland birds like the Henslow's sparrow (Ammodramus henslowii) require taller vegetation, upland sandpipers (Bartramia longicauda) require short grasses. One of Nachusa's goals in introducing bison was to create a more heterogeneous or patchy landscape. Continued measurement of VOR and aboveground biomass can help land managers know whether they are meeting this goal.

Fire and Grazing

Regularly applied prescribed fire is an important management tool in tallgrass prairie. In this study, time since last fire was a marginally significant covariate with plant community. Previous studies found fire to be a key disturbance regime that can influence the abundance and dominance of specific plants (Ewing and Engle 1988; Hulbert 1988). Nachusa actively manages the bison unit to include burned and unburned areas each year, and bison have free access to choose where they wish to graze. Prescribed fires at Nachusa are conducted in response to ecological need, not a strictly regimented rotation. We observe the bison actively grazing recently burned areas more than unburned areas, although a study of bison GPS locations in the first 2 y at Nachusa did not find a statistical correlation (Brockman et al. 2022). Rotating which areas are burned passively allows bison grazing pressure to shift across the landscape between years. Additional research is needed to evaluate if this is truly happening in practice. The less structured approach to fire management likely contributed to the marginal correlation between time since last fire and plant community in this study.

Future Directions

Future research will build on this work as the ecosystem continues to respond to bison presence. The bison herd at

Nachusa reached its desired stocking rate of 0.3-0.4 animal units/ha in 2018, part way through this study. As a result, grazing intensity has only been consistent for the last 2 y. This study's experimental design is intended to be long-term for continued monitoring of plant community changes as stocking rate stabilizes and the system continues responding. Additionally, we suggest any future study incorporate data on bison movement and grazing patterns in and around the surveyed plots. One option could include dung counts, which can be used to estimate relative density of animal presence and are a technologically simple means to account for bison use of surveyed plots (Ferretti et al. 2016). Dung counts have been used to estimate elephant numbers in forest communities, with a strong correlation between dung counts and habitat use (Barnes 2001). Bison GPS tracking would be an effective way to gain more detailed information on bison density and frequency in surveyed plots, building off Brockman et al. (2022).

Conclusions

Tallgrass prairie is one of the most exploited types of grassland in North America and 99% of the tallgrass prairie east and north of the Missouri River has been destroyed (Singh et al. 1983; Samson and Knopf 1994; Samson et al. 2004). Establishment and management to support remaining prairie remnants and create high-quality restorations is a top priority of conservation NGOs and government land managers. Places like Nachusa Grasslands are essential in this goal of protecting the legacy of the tallgrass prairie, and efforts evaluating management practices make it possible to ensure continue success of restoration efforts. Limited data have been collected on the effects of bison grazing in highly productive eastern tallgrass prairies, in contrast to the western grasslands.

In this study we show that bison have had minimal effect on diversity, abundance, and composition of vegetation at Nachusa since their introduction 5 y ago. Interactions of community type, grazing treatment, and year surveyed did not result in significant differences for the response variables of the Shannon-Wiener diversity index, ratio of grasses to forbs, ratio of nonnative to native species, VOR, or species composition. Future work will continue monitoring these permanent grazed and ungrazed plots to evaluate long-term ecosystem responses to bison through adaptive management.

ACKNOWLEDGMENTS

We acknowledge the people, both past and present, of the Peoria, Potawatomi, Meskwaki, Sauk, Myaamia, and Kiikaapoi. Dr. John Taft and Dr. Sara Baer were instrumental in designing the exclosure experimental design. Bill Kleiman, Cody Considine, and Jeff Walk have supported and encouraged this work from the beginning. This work was funded by The Nature Conservancy and Friends of Nachusa Grasslands.

Jennifer Chakravorty completed this research as part of her MS in Landscape Architecture (restoration ecology focus) from the University of Wisconsin-Madison. She currently works as a resource conservationist with the USDA-NRCS Regional Conservation Partnership Program supporting conservation on our private lands.

John A. Harrington is professor emeritus in the Department of Planning and Landscape Architecture where he specialized in restoration ecology and Midwestern grassland communities.

Elizabeth M. Bach is the Research Scientist at The Nature Conservancy's Nachusa Grasslands. She has a BA from Cornell College, MSc in Plant Biology from Southern Illinois University Carbondale, and PhD in Ecology & Evolutionary Biology from Iowa State University.

LITERATURE CITED

- Allred, B.W., S.D. Fuhlendorf, D.M. Engle, and R.D. Elmore. 2011. Ungulate preference for burned batches reveals strength of firegrazing interaction. Ecology and Evolution 1:132–144.
- Anderson, M.J., and D.C. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs 83:557–574.
- Anderson, R.C. 1970. Prairies in the prairie state. Transactions of the Illinois State Academy of Science 63:214–221.
- Anderson, R.C. 1990. The historic role of fire in North American grasslands. Pp. 8–18 *in* S.L. Collins and L.L. Wallace, eds. Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, OK.
- Anderson, R.C. 2006. Evolution and origin of the central grassland of North America: Climate, fire, and mammalian grazers. Journal of the Torrey Botanical Society 133:626–647.
- Archibald, S., W.J. Bond, W.D. Stock, and D.H.K. Fairbanks. 2005. Shaping the landscape: Fire–grazer interactions in an African savanna. Ecological Applications 15:96–109.
- Bamforth, D.B. 1987. Historical documents and bison ecology in the Great Plains. Plains Anthropologist 32:1–16.
- Barnes, R.F.W. 2001. How reliable are dung counts for estimating elephant numbers? African Journal of Ecology 39:1–9.
- Benkobi, L., D.W. Uresk, G. Schenbeck, and R.M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.
- Biondini, M.E., A.A. Steuter, and R.G. Hamilton. 1999. Bison use of fire-managed remnant prairies. Journal of Range Management 52:454–461.
- Blackburn, R.C., N.A. Barber, and H.P. Jones. 2020. Plant community shifts in response to fire and bison in a restored tallgrass prairie. Natural Areas Journal 40:218–227.
- Bragg, T.B. 1995. Climate, soils and fire: The physical environment of North American grasslands. Pp. 49–81 *in* K. Keeler and A. Joern, eds. The Changing Prairie. Oxford University Press, New York, NY.
- Briggs, J.M., and A.K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: Climate, soil moisture, topographic position, and fire as determinants of aboveground biomass.

 American Journal of Botany 82:1024–1030.
- Brockman, J.C., C.K. Nielsen, and J.W. Walk. 2022. Influences of land cover, fire, and human activity on bison habitat selection in restored grasslands. Rangeland Ecology and Management 84:45–53.
- Collins, S.L. 1992. Fire frequency and community heterogeneity in tallgrass prairie: A field experiment. Ecology 73:2001–2006.
- Collins, S.L. 2000. Disturbance frequency and community stability in native tallgrass prairie. American Naturalist 155:311–325.

- Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.
- Constible, J.M., R.A. Sweitzer, D.H.V. Vuren, P.T. Schuyler, and D.A. Knapp. 2005. Dispersal of non-native plants by introduced bison in an island ecosystem. Biological Invasions 7:699–709.
- Coppedge, B., and J. Shaw. 1998. Bison grazing prairie patterns on seasonally burned tallgrass. Journal of Rangeland Management 51:258–264.
- Corbett, E.A. 2004. A comparison of Illinois remnant prairies, 1976–1988. Proceedings of the North American Prairie Conferences 65:36–43.
- Curtis, J.T. 1959. The Vegetation of Wisconsin: An Ordination of Plant Communities. University of Wisconsin Press, Madison, WI.
- Daubenmire, R. 1959. Measurement of species diversity using canopy coverage classes. Northwest Science 33:43–66.
- Dixon, P. 2003. VEGAN, a package of R functions for community ecology. Journal of Vegetation Science 14:927–930.
- Ewing, A.L., and D.M. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. American Midland Naturalist 120:212–223.
- Ferretti F., L. Fattorini, A. Sforzi, and C. Pisani. 2016. The use of feces counts to estimate relative densities of wild boar in a Mediterranean area. Population Ecology 58:329–334.
- Flores, D. 1991. Bison ecology and bison diplomacy: The Southern Plains from 1800 to 1850. Journal of American History 78:465–485.
- Fuhlendorf, S.D., and D.M. Engle. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.
- Fuhlendorf, S.D., W.C. Harrell, D.M. Engle, R.G. Hamilton, C.A. Davis, and D.M. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.
- Fuhlendorf, S.D., D.M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. Biology 23:588–598.
- Grman, E., T. Bassett, and L. Brudvig. 2013. Confronting contingency in restoration: Management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. Journal of Applied Ecology 50:1234–1243.
- Grudzinski, B.P., M.D. Daniels, K. Anibas, and D. Spencer. 2016. Bison and cattle grazing management, bare ground coverage, and links to suspended sediment concentrations in grassland streams. Journal of the American Water Resources Association 52:16–30.
- Hartnett, D.C., K.R. Hickman, and L.E. Fischer Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49:413–420.
- Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46–58.
- Joubert, D., L.A. Powell, and W.H. Schacht. 2015. Visual obstruction as a method to quantify herbaceous biomass in southern African semi-arid savannas. African Journal of Range and Forage Science 32:225–230.
- King, K., A. Caven, K. Leung, D. Ranglack, and N. Archilla. 2019. High society: Behavioral patterns as a feedback look to social structure in plains bison (*Bison bison bison*). Mammal Research 64:365–376.
- Kleiman, B. 2016. Nachusa Grasslands: 30 years of lessons learned at Nachusa Grasslands. North American Prairie Conference Proceedings 9:137–141.
- Knapp, A.K., J.M. Blair, J.M. Briggs, S.L. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49:39–50.

- Leonard, S., J. Kirkpatrick, and J. Marsden-Smedley. 2010. Variation in the effects of vertebrate grazing on fire potential between grassland structural types. Journal of Applied Ecology 47:876–883.
- Lokonon, B.E., R. Beh Mba, M. Gbeha, and R. Glele Kakai. 2019. Parameters estimation methods in generalized linear mixed models (GLMMs) applied in ecology: A critical review. International Journal of Engineering and Future Technology 16:11–27.
- McHugh, T. 1972. The Time of the Buffalo. University of Nebraska Press, Lincoln, NE.
- McMillan, B.R. 2006. Records of early bison in Illinois. Illinois State Museum Scientific Papers 31:67–146.
- [NCEI] National Centers for Environmental Information. 2022. U.S. Climate Normals. Accessed 13 December 2022 from https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals-annualseasonal&timeframe=30>.
- Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, et al. 2020. vegan: Community ecology package. R package version 2.4-5.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, and J. Ranke. 2020. nlme: Linear and nonlinear mixed effects models. R package version 3.1-152.
- Powell, A.F.L.A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. Auk 123:183–197.
- Prentice, I.C. 1977. Non-metric ordination methods in ecology. Journal of Ecology 65:85–94.
- Pyne, S.J. 1982. Fire in America: A Cultural History of Wildland and Rural Fire. University of Washington Press, Seattle, WA.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.
- Robertson, K.R., R.C. Anderson, and M. Schwartz. 1997. The tallgrass prairie mosaic. Pp. 55–87 *in* M. Schwartz, ed. Conservation in Highly Fragmented Landscapes. Chapman and Hall, New York, NY.
- Rosas, C.A., D.M. Engle, J.H. Shaw, and M.W. Palmer. 2008. Seed dispersal by *Bison bison* in a tallgrass prairie. Journal of Vegetation Science 19:769–778.
- RStudio Team. 2020. RStudio: Integrated Development Environment for R. RStudio, Inc., Boston, MA.
- Samson, F.B., and F.L. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.
- Samson, F.B., F.L. Knopf, and W. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. Wildlife Society Bulletin 32:6–15.
- Schultz, B.B. 1985. Levene's test for relative variation. Systematic Zoology 34:449–456.
- Shaw, J.H. 1995. How many bison originally populated the western rangelands? Rangelands 17:148–150.
- Singh, J.S., W.K. Lauenroth, and D.G. Milchunas. 1983. Geography of grassland ecosystems. Progress in Physical Geography 7:46–80.
- Smith, M. 2008. Robel pole technique and data interpretation. Wyoming Facts. MP=111.10. University of Wyoming Cooperative Extension Service, Laramie, WY.
- Stewart, O.C. 1956. Fire as the first great force employed by man. Pp. 115–133 *in* W.L. Thomas, ed. Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, IL.
- [USDA USFS] USDA Forest Service, Rangeland Management Staff. 2009. Robel Pole Field Guide. Washington D.C.

- Vermeire, L.T., R.B. Mitchell, S.D. Fuhlendorf, and R.L. Gillian. 2004. Patch burning effects on grazing distribution. Journal of Range Management 57:248–252.
- Vinton, M.A., D.C. Hartnett, E.J. Finck, and J.M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10–18.
- Wilhelm, G., and L. Rericha. 2017. Flora of the Chicago Region: A Floristic and Ecological Synthesis. Indiana Academy of Science, Indianapolis, IN.
- Wilsey, B., and L. Martin. 2015. Top-down control of rare species abundances by native ungulates in a grassland restoration. Restoration Ecology 23:465–472.
- Winter, S.L., B.W. Allred, K.R. Hickman, S.D. Fuhlendorf. 2015. Tallgrass prairie vegetation response to spring fires and bison grazing. Southwestern Naturalist 60:30–35.
- Yazici, B., S. Yolacan. 2007. A comparison of various tests of normality. Journal of Statistical Computation and Simulation 77:175–183.