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Resource Availability and the Potential for Bison Introduction in a Landscape Mosaic

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Abstract.—The tallgrass prairie ecosystem was historically maintained through the interaction of climate, fire, and grazing by large ungulates. Efforts are being made to return large ungulates (bison) back into prairie landscapes, but successful introductions can be constrained by suitable habitat as determined by resource availability (plant biomass, forage quality of the plant biomass, and soil carbon and nitrogen), particularly given some of these tracts are former arable land that has been restored to tallgrass prairie. The objective of this study was to quantify whether plant biomass (available forage) differs between prairie types, if forage quality varies across native prairie remnants and restored prairies, and if these differences are related to carbon and nitrogen storage in soil. We sampled native prairie remnants, low seeded-diversity older restored prairies, and high seeded-diversity younger restored prairies at Nachusa Grasslands, Illinois during July 2014. Total plant biomass differed between the three prairie types, with the high seeded-diversity younger-restored prairies having almost twice that of the low seeded-diversity older-restored prairies and more than twice that of the remnant prairies. In regard to forage quality, the percentage of crude protein in dry matter was greater in the remnant prairies compared to both of the restored prairie types. The high seeded-diversity younger restored prairies had the highest lignin concentration in the forage. The fat content of forage was highest in the high seeded-diversity younger-restored prairies. Total soil carbon and nitrogen did not differ between the three prairie types at either the 0–10 cm or 10–20 cm depth. The preliminary findings of this study suggest bison grazing within the introduction unit at Nachusa Grasslands will be more intensive within restored prairies as compared to remnants.

Introduction

The principle drivers in formation and maintenance of the tallgrass prairie ecosystem in North America were climate, fire, and grazing by large ungulates (Anderson, 2006). Bison, in particular, were the dominant grazers prior to European settlement and play a "keystone" role in the maintenance of biodiversity through their wallowing behavior and preferential grazing on graminoids (grasses and sedges) (Knapp *et al.*, 1999; McMillan *et al.*, 2011; Collins and Calabrese, 2012). Today, thanks to conservation efforts there are ~500,000 bison, but over 90% of the bison herds in North America reside on privately or commercially owned land (Sanderson *et al.*, 2008). Despite this great success in the recovery of bison numbers from near extinction, less than 21,000 bison are managed as conservation herds, with less than 8% ranging on >2000 km^2 (Kohl *et al.*, 2013). While their role in tallgrass prairie ecosystems has been greatly reduced, bison have been introduced into three large preserves restored from cultivation, Neal Smith National Wildlife Refuge in Iowa, Nachusa Grasslands in Illinois and Kankakee Sands in Indiana. These preserves are a

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landscape mosaic of restored and remnant prairies, and the introduction of bison is an attempt to compliment prescribed burning and restore the historical role of grazing and fire to ecosystem function.

One of the necessary components for bison introduction is the availability of suitable habitat that can sustain a breeding population (Steenweg *et al.*, 2016), determined in large part by the availability of plant biomass. Optimal foraging theory postulates access to higher quality resources (*i.e.* plant biomass) leads to larger group sizes (Hirth, 1977). In comparison to cattle, bison require grazing areas with an intermediate amount of plant biomass (Kohl *et al.*, 2013). Bison preferentially graze on graminoids, which typically have lower quality forage relative to forbs (Coppedge *et al.*, 1998), and previous studies have found diet will shift seasonally based on the availability of C3 and C4 grasses (Vinton *et al.*, 1993; Post *et al.*, 2001; Raynor *et al.,* 2016). In Yellowstone National Park, it was found male and female bison diet differed considerably during the mating season, as female diet consisted primarily of high quality forage and males exhibited greater forage breadth (Berini and Badgley, 2017). In the Neal Smith National Wildlife Refuge, sexual differences in bison foraging behavior occur in which mixed age and female animals preferentially grazed recently burned areas – selecting forage quality over quantity (Kagima and Fairbanks, 2013).

Forage quality has been defined as the overall nutritional value of a plant and how efficiently a grazer can convert forage into mass containing carbohydrates, fats, and proteins (Linn and Martin, 1999). Forage quality likely varies between remnant and restored prairies because there is less storage of nutrients (nitrogen) in soil that has been cultivated (McLauchlan *et al.*, 2006; Matamala *et al.*, 2008; Baer *et al.*, 2010), and foliar nitrogen was shown to be higher in prairie grass growing in remnant prairie compared to restored prairie (Baer *et al.*, 2005). Cultivating prairie lowers soil organic matter (Anderson and Coleman, 1985) that supplies most of the nitrogen (N) to plants for protein synthesis. Plant proteins account for most of the N transferred to grazers. By this logic prairie restored from long-term cultivation likely produces biomass with lower N content an important determinant of forage quality.

Previous research at Nachusa Grasslands in Illinois has demonstrated N storage in cultivated soil is $\sim$40% of native prairie remnants and total soil N shows negligible change from cultivated levels following 20 y of prairie restoration (Hansen and Gibson, 2014; Klopf *et al.*, 2017). Despite this low storage of N in the soil, aboveground productivity was similar among prairies restored for $>$4 y (Klopf *et al.*, 2017). Productivity of restored (relative to native) prairie likely contains lower N because root biomass increases over time and the amount of N relative to carbon in roots declines as restoration proceeds (Klopf *et al.*, 2017). In addition the quality of roots declines as restorations age and becomes lower than native prairie (Klopf *et al.,* 2017). If root nutrient concentrations reflect N in aboveground tissue, then the quality of forage should also decline with restoration age. The N content of aboveground biomass is known to vary among species, functional groups (cool-season or C_3 plants are more nutritious than warm-season or C_4 plants), management (higher following burning of areas that have not recently burned), and season (Mattson, 1980; Hooper and Vitousek, 1997; Ranglack and du Toit, 2015). Knowledge of N content (derived from soil) and caloric content (derived from photosynthesis) of forage will be valuable for understanding the performance of bison on a restored landscape, as crude fiber and protein in forage have been key parameters in explaining the behavior and performance of cattle in grassland (Stejskalová *et al.*, 2013) and bison in restored prairie (Kagima and Fairbanks, 2013).

Prior to bison introduction at Nachusa Grasslands in October 2014, no research had been conducted to quantify potential differences in available plant biomass, forage quality, and soil carbon and nitrogen (as it is related to aboveground plant biomass) across the introduction area and how this could impact future bison grazing. Plant biomass, forage quality, and soil carbon and nitrogen are likely heterogeneous across landscapes containing restored and remnant prairies with potential consequences for the distribution, localized grazing intensity, and performance of introduced bison. The objective of this study was to quantify whether the availability of plant biomass and forage quality varies across three categories of prairie sites (native prairie remnants, low seeded-diversity older-restored, and high seeded-diversity younger-restored sites) and whether it is related to C and N storage in soil. We postulate there will be higher available plant biomass for forage in the restored prairies compared to the remnant prairies and there will be lower forage quality, with less nitrogen and crude protein, in restored sites relative to remnant prairie, attributed to lower N storage in the soil.

MATERIALS AND METHODS

STUDY SITE

The study was conducted at Nachusa Grasslands (41°53′27″N, 89°20′34″W) located in Lee and Ogle counties, Illinois. Nachusa is comprised of ~2000 ha of restored and remnant prairie, oak savanna, and agricultural land managed by the Nature Conservancy. Mean annual precipitation since 1985 was 975 mm of which an average of 644 mm fell during the growing season (April 1–September 30) (30 y record, Franklin Grove, IL; www.ncdc.noaa.gov/cdo-web). Average annual temperature from 1985–2014 was 9.1 C (average minimum and maximum temperatures were 3.6 C and 14.7 C) (30 y record, Franklin Grove, Illinois). The soils at the preserve were a mixture of sandy and silt loams formed by the erosion of sandstone, glacial outwash, and loess deposits (Taft *et al.*, 2006). The soils were characterized as fine-loamy, mixed mesic Typic Arguidolls and Typic Hapludalfs and fine-loamy, over sandy or sandy-skeletal mixed mesic Typic Hapludolls (Elmer and Zwicker, 2005).

We sampled native prairie remnants (Rem) ($n = 3$), low seeded-diversity older restored prairies (LD) ($n = 3$), and high seeded-diversity younger restored prairies (HD) ($n = 3$) for plant biomass, forage quality, and soil carbon and nitrogen in July 2014. The LD prairies were restored >15 y prior to sampling, and the HD prairies were restored <5 y prior to sampling. Counterparts for the LD and HD restored prairies were not available due to the restoration history at Nachusa Grasslands. The restoration procedure initially used seed mixes that were graminoid heavy, but around 1999 the site managers started using seed mixes that were more diverse and included a greater forb to graminoid ratio in regards to species numbers and total weight. Each restoration initially received a heavy seeding (13.5 kg ha-1 of seed of which 11.3 and 2.3 kg were forb and graminoid species, respectively) of native species collected from the preserve during the winter followed by overseeding the following year. The seeded species pool generally consisted of 75 forb and 15 graminoid species (although this number varied year to year based on the yield of seed collected from restored and remnant prairie) (Willand *et al.*, 2013; Klopf *et al.*, 2017). Together these seed mixtures are an attempt to represent the plant community composition of the remnant prairies on Nachusa. In order to maintain the structure and function of the restored and remnant prairies, site managers control invasive plant species as necessary and conduct prescribed burns every 12–18 mo. Burn units range in size from 5 to 300 acres, and multiple units are often burned on the same day during either the fall or spring. Complete burn reports from

TABLE 1.—Coordinates for the starting point of each baseline transect sampled for forage quality/ biomass and soil at Nachusa Grasslands, Illinois

Site	Latitude	Longitude
High seeded-diversity younger prairie 1 (HD 1)	N41°53.931′	W89°22.009′
High seeded-diversity younger prairie 2 (HD 2)	N41°54.019′	W89°22.014′
High seeded-diversity younger prairie 3 (HD 3)	N41°53.915′	W89°20.764′
Low seeded-diversity older prairie 1 (LD 1)	N41°53.787′	W89°21.801′
Low seeded-diversity older prairie 2 (LD 2)	N41°53.782′	W89°21.461′
Low seeded-diversity older prairie 3 (LD 3)	N41°53.929′	W89°21.225′
Prairie remnant 1 (Rem 1)	N41°53.926′	W89°21.560′
Prairie remnant 2 (Rem 2)	N41°53.920′	W89°21.644′
Prairie remnant 3 (Rem 3)	N41°53.839′	W89°21.677′

fall 2009–spring 2018 are available at https://www.nachusagrasslands.org/controlled-burns. html.Within each field three 50 m sampling transects (n = 9 per prairie type) were established along a 50 m baseline transect (Table 1). The transects were established at random distances along the baseline transect. Due to the small size of the remnant prairies, the length of each baseline transect in these fields was modified to fit the widest axis. Five 0.10 m^2 frames were placed 10 m apart along each transect starting from the 10 m point on each transect to sample plant biomass and soil (n = 15 for each field). We chose 0.10 m^2 frames for our sampling because this size quadrat is commonly used in tallgrass prairie to quantify aboveground vegetation (Briggs and Knapp, 1991). The entire study site was burned in April 2014 (B. Kleiman, pers. comm.).

PLANT BIOMASS AND FORAGE QUALITY

All plant biomass rooted within the 0.10 m^2 frames along each transect was clipped at ground level and sorted by forbs, graminoids (grasses and sedges), and litter. Litter was collected to discern any biomass that was not burned during the spring from the current year's biomass but were not included in our statistical analyses. It should be noted, because our collection was not during the peak of the growing season (late August–September), we did not quantify above net primary productivity (ANPP). Biomass samples were dried at 60 C, weighed, composited by transect (graminoid and forb samples were kept separate), and later ground. A subsample was analyzed for percent N at Southern Illinois University Carbondale and a second subsample was sent to the University of Wisconsin Madison Soil and Forage Laboratory to analyze for acid detergent fiber and neutral detergent fiber, lignin, NDF digestibility, in vitro dry matter, crude protein content, and fat content to determine the overall digestibility of the forage. Acid detergent fiber and neutral detergent fiber analyses represent the digestible and indigestible components of forage (cellulose, hemicellulose, and lignin). Neutral detergent fiber digestibility (NDFD) represents both animal consumption and forage energy content. Dry matter is the percentage of forage that is not water.

SOIL CARBON AND NITROGEN

One 2 cm diameter soil core was taken at a depth of 20 cm (separated into 0–10 cm and 10–20 cm to compare to previous studies) (n = 5 per transect) following clipping within the area of the frame. Soil cores were composited by depth and transect. In the laboratory soil cores were homogenized through a 4 mm sieve. Two 50 g subsamples were dried at 55 C and ground to a fine powder. From each subsample 50–100 mg was analyzed for percent C and N with a Thermo Scientific Flash 1112 CN Analyzer distributed by CE Elantech Corporation (Lakewood, New Jersey) in the SIUC Core Facility. Percent C and N were converted to volumetric amounts based on equivalent mass determined from bulk density cores. We measured bulk density of soil from three (1 per transect) 5.5 cm dia. x 20 cm deep (separated into 0–10 cm and 10–20 cm to compare to previous studies) intact soil cores dried to a constant mass at 105 C and weighed.

STATISTICAL ANALYSES

Plant biomass, forage quality, and soil carbon and nitrogen were analyzed using a one-way analysis of variance (PROC ANOVA) in SAS (SAS version 9.3 2011). A Tukey-Kramer test (MSD) was used for all pair-wise comparisons if the results of the ANOVA were significant. Prairie type was the independent variable for our study. Biomass and forage quality variables were analyzed separately. Total biomass analyses were taken from the combination of graminoid and forb biomass. Significance was assigned at $\alpha = 0.05$.

RESULTS

PLANT BIOMASS

There was not a significant difference in graminoid biomass between the three prairie types ($P > 0.05$) (Fig. 1A). Although the difference was not statistically significant, there was greater graminoid biomass in restored prairies (73% of the graminoid biomass) compared to remnant prairies (27% of the graminoid biomass (Fig. 1A). Forb biomass differed between the three prairie types ($F_{2,6} = 4.93$, $P = 0.054$) (Fig. 1B) with the greatest forb biomass in the HD prairies (58% of the total forb biomass) compared to the LD prairies (35% of the total forb biomass) and remnant prairies (7% of the total forb biomass). Total biomass also differed between the three prairie types ($F_{2,6} = 64.10$, $P < 0.001$) (Fig. 1C). Total biomass in the HD prairies was almost twice that of the LD prairies and more than twice that of the remnant prairies (Fig. 1C).

FORAGE QUALITY

There was not a significant difference in dry matter, neutral and acid detergent fiber, and neutral detergent fiber digestibility between the three prairie types ($P > 0.05$) (Figs. 2A–D; Table 2). The percentage of lignin in dry matter was greatest in the HD prairies compared to both the LD and remnant prairies ($F_{2,6} = 6.06$, $P = 0.009$) (Fig. 2E). The percentage of crude protein in dry matter was significantly greater in the remnant prairies compared to both of the restored prairies ($F_{2,6} = 11.51$, $P < 0.001$) (Fig. 2F). The fat content of forage differed between the three prairie types ($F_{2,6} = 5.33$, $P = 0.015$) (Fig. 2G) with the greatest fat content available in the HD prairies.

SOIL CARBON AND NITROGEN

There were no significant differences between the three prairie types in either total soil C (Figs. 3A, C) or total soil N (Figs. 3B, D) at either the 0–10 cm or the 10–20 cm depth ($P > 0.05$; Table 2). However, total soil N was higher in restored prairies than in remnant prairies at both soil depths.

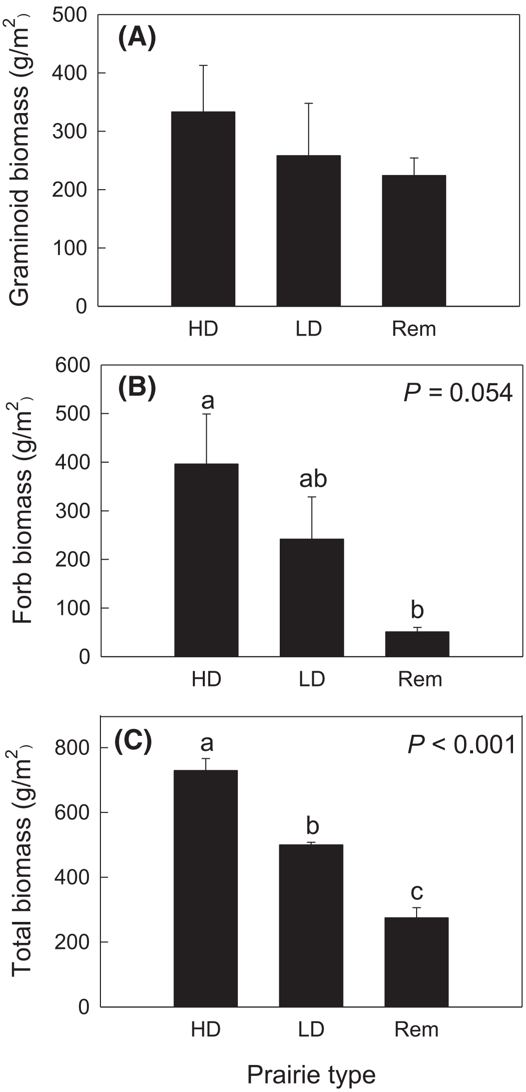

FIG. 1.—Mean (±SE) (**A**) graminoid, (**B**) forb, and (**C**) total aboveground biomass from transects sampled in high diversity-seeded younger-restored (HD), low diversity-seeded older-restored (LD) and remnant (Rem) prairies at Nachusa Grasslands, Illinois. Means accompanied by the same letter were not significantly different ($\alpha = 0.05$)

DISCUSSION

Plant diversity and productivity in tallgrass prairie is typically attributed to the availability of nitrogen in the soil (Seastedt and Knapp, 1993). Historically, nitrogen availability on prairie landscapes was modulated by the interaction between fire frequency and grazing by native ungulates (Collins, 1987). The composition and functioning of tallgrass prairie has

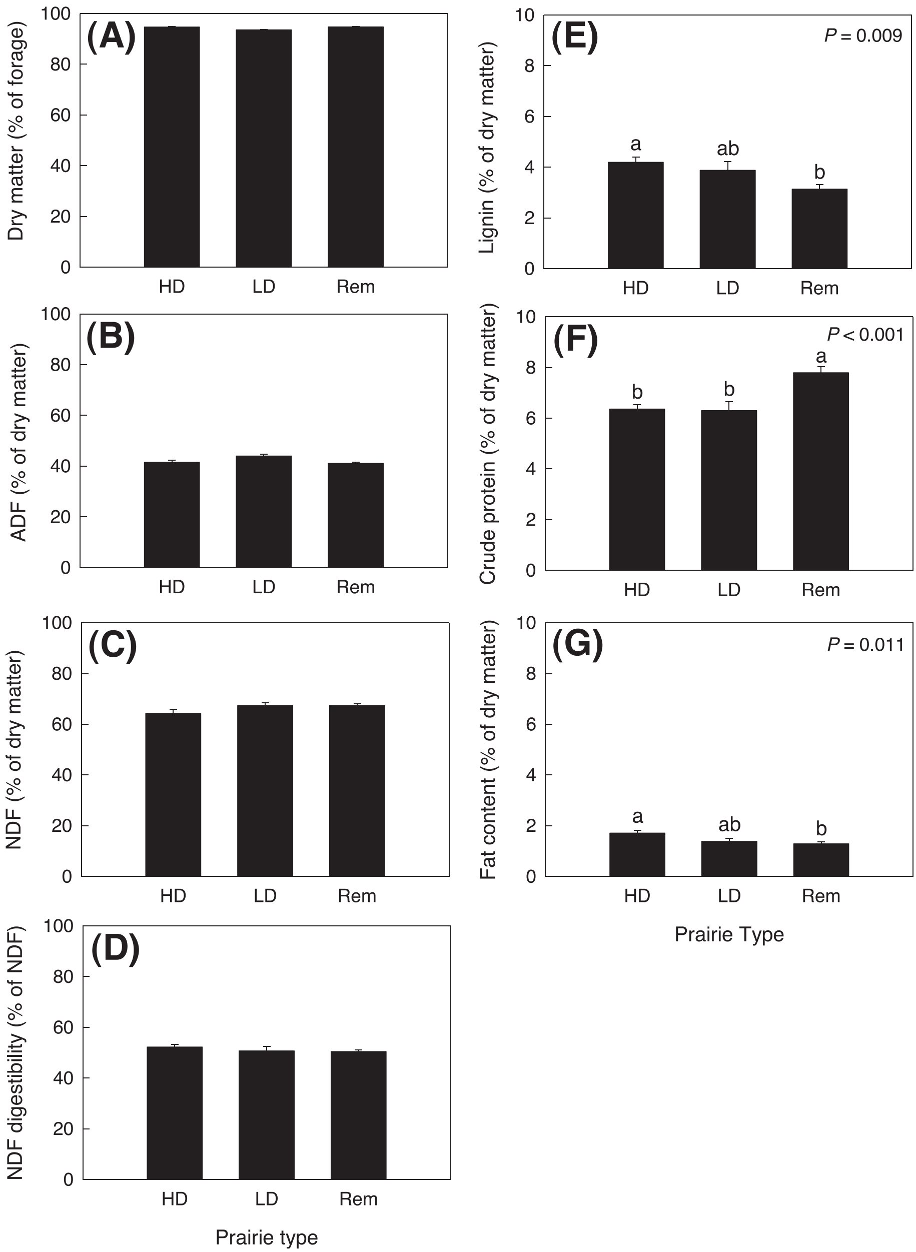

FIG. 2.—Forage quality as quantified by mean (±SE) (**A**) dry matter, (**B**) acid detergent fiber (ADF), (**C**) neutral detergent fiber (NDF), (**D**) NDF digestibility, (**E**) lignin, (**F**) crude protein, and (**G**) fat content from transects sampled in high diversity-seeded younger-restored (HD), low diversity-seeded older–restored (LD) ,and remnant (Rem) prairies at Nachusa Grasslands, Illinois. Means accompanied by the same letter were not significantly different ($\alpha = 0.05$)

TABLE 2.—Summary statistics (F values with degrees of freedom as subscripts) for plant biomass, forage quality, and soil carbon and nitrogen from high seeded-diversity younger prairies (HD), low seeded-diversity older prairies (LD), and prairie remnants (Rem) sampled within the bison introduction unit at Nachusa Grasslands, Illinois. Pair-wise comparisons are provided where P < 0.05 for prairie type. * = P < 0.05; ** = P < 0.01; *** = P < 0.001

	Prairie type	HD vs. LD	HD vs. Rem	LD vs. Rem
Plant Biomass				
Graminoid biomass	$0.61_{2,6}$	—	—	—
Forb biomass	$4.93_{2,6}$ *	1.40	3.14*	1.73
Total biomass	$64.10_{2,6}$***	5.72**	11.32***	5.60**
Forage quality				
Dry matter	$0.32_{2,6}$	—	—	—
Acid detergent fiber	$0.64_{2,6}$	—	—	—
Neutral detergent fiber	$2.55_{2,6}$	—	—	—
NDFD	$0.75_{2,6}$	—	—	—
Lignin	$6.06_{2,6}$**	1.29	3.18	4.75**
Fat	$5.33_{2,6}$*	3.17	0.96	4.51**
Crude protein	$11.51_{2,6}$ ***	0.22	5.71*	5.73*
Soil C and N				
Total C 0–10 cm	$1.05_{2,6}$	—	—	—
Total C 10–20 cm	$1.03_{2,6}$	—	—	—
Total N 0–10 cm	$2.07_{2,6}$	—	—	—
Total N 10–20 cm	$3.23_{2,6}$	—	—	—

been modified by the loss of keystone species (*i.e.* native grazers), habitat fragmentation, increased atmospheric nitrogen deposition, and altered fire frequencies (Samson and Knopf, 1994). Contrary to our initial predictions, agricultural legacy does not appear to have any negative impacts on plant biomass, forage quality, and total carbon and nitrogen within the introduction unit at Nachusa Grasslands.

Contrary to our original prediction, there was greater plant biomass in the restored prairies compared to the remnant prairies. Klopf *et al.* (2017) found similar results for total aboveground net primary productivity (ANPP) between low and high diversity-seeded prairie restorations at Nachusa Grasslands, whereby total ANPP did not change significantly over time during restoration. The similarity in graminoid biomass among prairie types is not surprising considering both the restored and remnant prairies are dominated by C4 grass species such as big bluestem (Andropogon gerardii Vitman), Indiangrass [Sorghastrum nutans (L.) Nash], and little bluestem [Schizachyrium scoparium (Michx.) Nash]. Smith and Knapp (2003) found these dominant C4 grasses can have a strong influence on ecosystem processes such as aboveground net primary productivity in tallgrass prairie through their competitive interactions with the subordinate plant community. Forb biomass was significantly greater in the restored prairies compared to the remnant prairies, particularly in the HD prairies. The stark differences in forb biomass between prairie types can be attributed to the seed mixes used during restoration. While total biomass was higher in the restored prairies, this was driven by greater forb biomass. Again, this can be attributed to the restoration history at Nachusa Grasslands in which more diverse seed mixes were applied to the younger restored prairies leading to greater forb diversity in the aboveground plant community (and plant biomass). Our findings suggest available plant biomass within

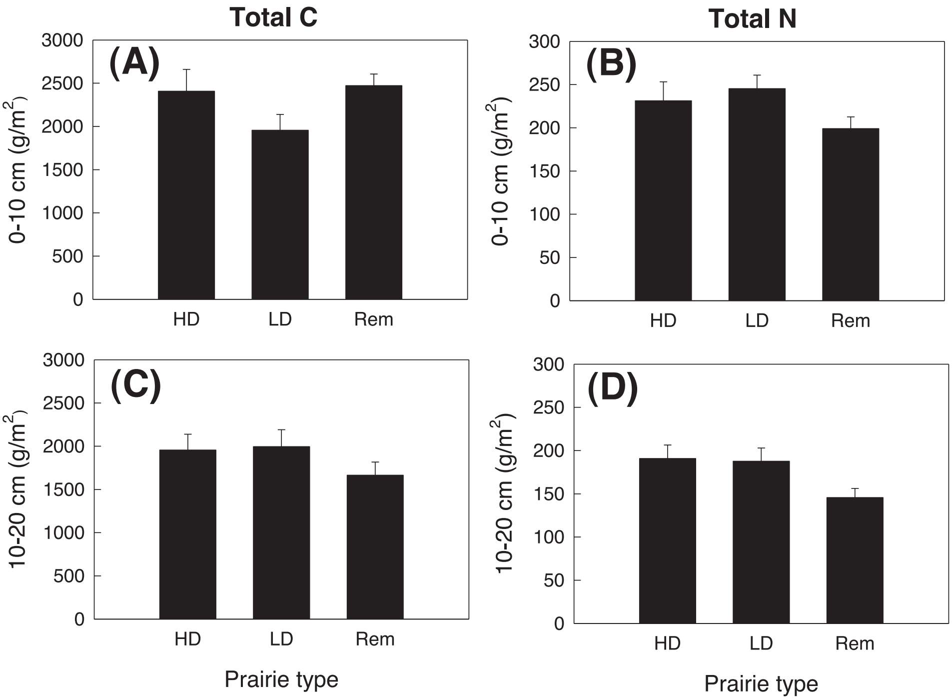

FIG. 3.—Mean (±SE) total carbon collected from (**A**) 0–10 cm and (**C**) 10–20 cm and total nitrogen collected from (**B**) 0–10 cm and (**D**) 10–20 cm depths along transects sampled in high diversity-seeded younger-restored (HD), low diversity-seeded older–restored (LD) and remnant (Rem) prairies at Nachusa Grasslands, Illinois

the bison introduction unit at Nachusa Grasslands is heterogeneous with higher quantities in the restored prairies.

While the availability of forage may be similar between the three prairie types sampled during this study, there were differences in the nutritional quality of the graminoid forage. Our findings suggest graminoid forage quality increases during restoration but do not reach levels equivalent with native prairie. We hypothesized soils with higher nitrogen storage (*i.e.* remnant prairie) would also have higher forage quality. Our findings did not find a relationship between soil nitrogen and forage quality, as remnant prairies had lower total nitrogen content but higher forage quality than the restored prairies. This could result from much longer established vegetation in the native prairie accumulating N inputs from atmospheric deposition and greater microbial activity in older soils (Bach et al., 2010).

While differences exist in the nutritional quality of forage between restored and remnant prairies, this may be alleviated for short time periods by management practices. Previous studies have documented an increase in forage quality (particularly crude protein) following prescribed burning (Biondini *et al.*, 1999; Alfred *et al.*, 2011; McGranahan *et al.*, 2014; Raynor *et al.*, 2016). The increase in forage quality following prescribed burning can be sustained for several years with moderate grazing (Milchunas *et al.*, 1995) and in some cases upwards of a decade following burning (Ranglack and du Toit, 2015). Our entire study site was burned in April 2014, 3 mo before we conducted our sampling. Due to the burning, our results for plant biomass, forage quality, and total carbon and nitrogen may be higher than normal. However, because the entire study site received the same treatment, we can assume that this is not the primary driver of the differences observed for plant biomass, forage quality, and total carbon and nitrogen between prairie types. The current prescribed burning regime every 12–18 mo in both restored and remnant prairies at Nachusa Grasslands may be sufficient to prevent overexploitation of any one area by bison and promote heterogeneous grazing patterns.

Total carbon and nitrogen did not vary significantly between restored and remnant prairies. This is again contrary to our original hypothesis that remnant prairies would have higher soil carbon and nitrogen than restored prairies. The similarity in total carbon and nitrogen between restored and remnant prairies may be the result of plant species composition more than agricultural legacy. Klopf *et al.* (2017) found root biomass and root nitrogen storage increased during restoration to levels comparable to remnant prairie. This may explain why there was little difference in total soil carbon and nitrogen between restored and remnant prairies. Another factor that may have contributed to the similarity in total soil carbon and nitrogen is plant cover. Willand *et al.* (2013) found plant cover was similar, or in some cases greater, in restored prairies compared to remnant prairies at Nachusa Grasslands. Plant cover may be correlated with similar or greater soil carbon and nitrogen in restored prairies due to the inputs of carbon and nitrogen from plant biomass and greater root stocks belowground from higher densities of plants in restored prairies compared to remnant prairies. Another possible explanation may reside in the soil itself. The restored prairies were cultivated in the past because they contain deeper soils that were richer in organic materials compared to the remnant prairies. The remnants we sampled had never been cultivated because they have fairly shallow soils which may explain the lower pools of available carbon and nitrogen.

The preliminary findings of this study suggest bison grazing within the introduction unit at Nachusa Grasslands may be more intensive within the restored prairies because there is more plant biomass available and forage quality (in regards to crude protein) was only slightly higher in remnant prairies. However, predicting how bison will graze within the introduction unit at Nachusa Grasslands is difficult. Some factors that need to be considered are the dietary preferences of male and female bison and what role fire may have in creating a heterogeneous landscape for grazing. Post introduction research will need to be conducted to examine how bison are utilizing the restored and remnant prairies and the effects their introduction have on plant community composition and stored soil resources.

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