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Abstract. Areas with relatively high spatial heterogeneity generally have more biodiversity than those that are spatially homogeneous areas due to increased potential as habitat. Management practices such as controlled grazing also affect the biodiversity in grasslands, and we hypothesize that this is due in part to the impacts of variation in grazing on plant heterogeneity and its spatial patterns. Understanding these mechanisms is important for designing an effective grazing system from a livestock management point of view. We used satellite-based, above-ground, live plant biomass (ALB) estimates at a pasture scale, in an experimental area located across the border of the East Block of Grasslands National Park (GNP) and an adjacent community pasture, to assess the effects of 5 intensities of grazing on the spatiotemporal pattern of ALB in mixed grasslands. Overall, heterogeneity increased with grazing intensity, whereas the spatial range decreased, except at the highest intensity, which had no impact on heterogeneity.

Résumé. Les zones à relativement forte hétérogénéité spatiale ont généralement une plus grande biodiversité que les zones spatialement homogènes en raison de l'habitat potentiel accru. Les pratiques de gestion telles que le pâturage contrôlé influencent également la biodiversité dans les prairies. Nous émettons l'hypothèse que cela est dû en partie à l'impact des variations du pâturage sur l'hétérogénéité de la végétation et ses structures spatiales. La compréhension de ces mécanismes est importante pour la conception d'un système de pâturage efficace d'un point de vue de la gestion du bétail. Nous avons utilisé des estimations satellitaires de la biomasse végétale vivante aérienne à l'échelle du pâturage dans une zone expérimentale située à la frontière du bloc Est du parc national des Prairies «GNP» et un pâturage communautaire adjacent pour évaluer les effets de 5 intensités de pâturage sur la structure spatio-temporelle de la biomasse végétale vivante aérienne dans les prairies mixtes. Dans l'ensemble, l'hétérogénéité a augmenté avec l'intensité du pâturage tandis que la portée spatiale a diminué, sauf à la plus haute intensité qui n'a eu aucune incidence sur l'hétérogénéité.

INTRODUCTION

Grasslands have developed under the influence of grazing so the proposition seems reasonable that grazing disturbance is necessary to maintain the ecological integrity in the grassland ecosystem (Walter et al. 2002; Vermeire et al. 2004). When grazing is maintained properly, it can be an excellent management tool for maintaining primary production, biodiversity, and habitat structure (Hobbs 1996; Collins et al. 1998). In contrast, improper grazing management, such as overgrazing, can not only negatively affect productivity, but also cause severe loss of soil fertility (Lauenroth et al. 1999; Fuhlendorf and Engle 2004). For example, large numbers of livestock can reduce plant biomass and cover because of surface soil compaction through trampling, which can decrease the soil's water infiltration capacity, resulting in increased runoff, soil erosion, and carbon losses

from the soil. Management decisions with regard to length of grazing and rest periods influence the soil water content, which can vary substantially as a result of animal impact and duration of grazing, despite similar vegetation cover and soil type (Weber and Gokhale 2011).

Depending on the grazing intensity and level of plant productivity, grazing activity can either increase or decrease the spatial heterogeneity of vegetation by changing the vegetation structure and height, thus affecting the biodiversity of a region (Knapp et al. 1999; Truett et al. 2001; Derner et al. 2009). Studies have shown that diverse mixtures of prairie plants produce more biomass and sequester more carbon compared to monocultures (Vermeire et al. 2004). Understanding the effects of variation in grazing intensity (or utilization rates) on spatial patterns of plant biomass and productivity can help in designing grazing management systems that benefit conservation of different plant and animal species within a mixed grassland ecosystem.

We examined the effects of cattle grazing intensity on the spatiotemporal pattern of aboveground live plant biomass (ALB) in a mixed grassland ecosystem using satellite-based ALB estimates at a pasture scale. The mixed grassland ecosystem in Canada is important for carbon storage, soil organic matter conservation, and the richness and unique aspects of its biodiversity; it is home to threatened species such as the only remaining black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Canada, swift fox (*Vulpes velox*), ferruginous hawk (*Buteo regalis*), and hairy prairie-clover (*Dalea villosa var. Villosa*). However, the spatial pattern of vegetation and its response to varying degrees of grazing intensity is poorly understood.

We hypothesized that the spatial heterogeneity of ALB for grazed pastures would be higher compared to ungrazed pastures, due to the selective behavior of cattle (e.g., Hartnett et al. 1996; Townsend and Fuhlendorf 2010) and would increase over time in response to grazing intensity because heterogeneity in ALB is positively related to grazing intensity. In ecological studies, the highest heterogeneity at intermediate grazing intensity is well accepted (Hart 2001; Bai et al. 2001). Furthermore, we expected an impact of slope position, with downslope having more heterogeneity because of preferential grazing by cattle in areas near water and shallower slopes (e.g., Pinchak et al. 1991; Fortin et al. 2003).

MATERIALS AND METHODS

Study Area

Grasslands National Park of Canada (GNP) was established in 1988 near the Saskatchewan–Montana border to preserve a representative portion of the remaining native northern mixed grass prairie ecosystem. Land acquisition for the park started in 1984, before park establishment, and is still underway. The park is comprised of 2 areas, referred to as the East Block and the West Block, of relatively undisturbed mixed grass prairie.

The region's climate is dry subhumid to semiarid and has long cold winters and short hot and dry summers. During the summer, average temperatures range between 20°C and low 30s°C. The mean annual precipitation is approximately 350 mm, with potential annual evapo-transpiration of approximately 347 mm (Parks Canada 2002). Approximately one-third of this total annual precipitation falls as snow during the winter, whereas the rest of it falls as rain, mostly during the summer. Winds are strong and frequent, particularly in the spring (Coupland 1991). The climatic conditions produce an environment that supports a unique flora and fauna, including rare plant species such as dwarf fleabane (*Conyza ramosissima)*, Bessey's locoweed (*Oxytropis besseyi*), squirrel tail grass (*Hordeum jubatum*), and Canada's only black-tailed prairie dogs (*Cynomys ludovicianus*). Sage, clubmoss (*Selaginella densa*), lichens and cacti (*Cactaceae*) also form a significant part of the plant community in the drier locations. The park also supports pronghorn antelope, mule deer, elk, coyotes, and numerous small mammals such as white-tailed jackrab-

bit (*Lepus townsendii*) and the Richardson's ground squirrel (*Urocitellus richardsonii*) (Parks Canada 2002).

The research was carried out in the East Block of GNP (Latitude: 49° 01′ N, Longitude: 106° 49′ W, Elevation: 800 m) and the adjacent Mankota community pasture (government-owned and -managed land used for communal grazing by local ranchers) located in southern Saskatchewan, Canada (Figure 1). The East Block of the GNP has been ungrazed since its acquisition of land in 1984. The study area consists mainly of open, rolling, upland prairie interspersed with riparian lowland and creeks. The vegetation is mainly characterized as northern mixed-grass prairie. In addition to short to medium grass species (e.g., blue grama grass (*Bouteloua gracilis*) and northern and western wheatgrasses (*Elymus lanceolatus and Pascopyrum smithii*)), the block also has forbs (e.g., scarlet mallow (*Sphaeralcea coccinea*) and moss phlox (*Phlox hoodii*)) and shrubs (e.g., wild prickly rose (*Rosa acicularis*) and silver sagebrush (*Artemisia cana*)), which are scattered across the landscape. During the field work in summer 2008, presence of death camas (*Zigadenus venenosus*) was also noticed in some pastures in the East Block, which is avoided by cattle because it is poisonous.

Soils vary from orthic brown chernozems to saline regosols and solonetz, depending on the landscape. For example, loamy, orthic brown chernozems dominate the upland areas, whereas valley soils are a complex of fine saline regosols, solonetz, and chernozems (Saskatchewan Institute of Pedology 1992).

Because grassland ecosystems were regulated by disturbances such as frequent and extensive fires and intensive grazing by bison, to maintain high species diversity in the remaining grassland areas, disturbances must now be provided through active management (Walter et al. 2002; Vermeire et al. 2004). A biodiversity and grazing experiment (BGE) with a Before–After Control–Impact design was started in 2006 as collaboration between Parks Canada and researchers from the University of Manitoba (Koper et al. 2008) and Carleton University.

As shown in Figure 1, the experimental area includes nine ∼300 ha pastures (P1 to P9) in the East Block of the park and 4 controlled grazing pastures (pastures *P10, P11, P12, P13*) in the adjacent Mankota community pasture, the latter functioning as long-term grazed control pastures for the study. All 4 of these experimental pastures on the Mankota community pasture were fenced, resulting in controlled grazing instead of the preexisting free range grazing until 2008.

Grazing intensity here refers to the cumulative effect grazing animals have on the land during a particular time period, expressed as percent utilization in this study. Here percent utilization is the percentage of the current year's primary production consumed or destroyed by livestock (Holechek et al. 2001). In June 2008, yearling steers were introduced to the experimental pastures at stocking rates predicted to result in average annual forage utilization rates ranging from 20% to 70% (20% = very light grazing intensity (P2); 33% = light grazing intensity (P6); 45%–50% = low moderate grazing intensity (P7, P10 – P13); 57% = high moderate grazing intensity (P3); and 70% = heavy
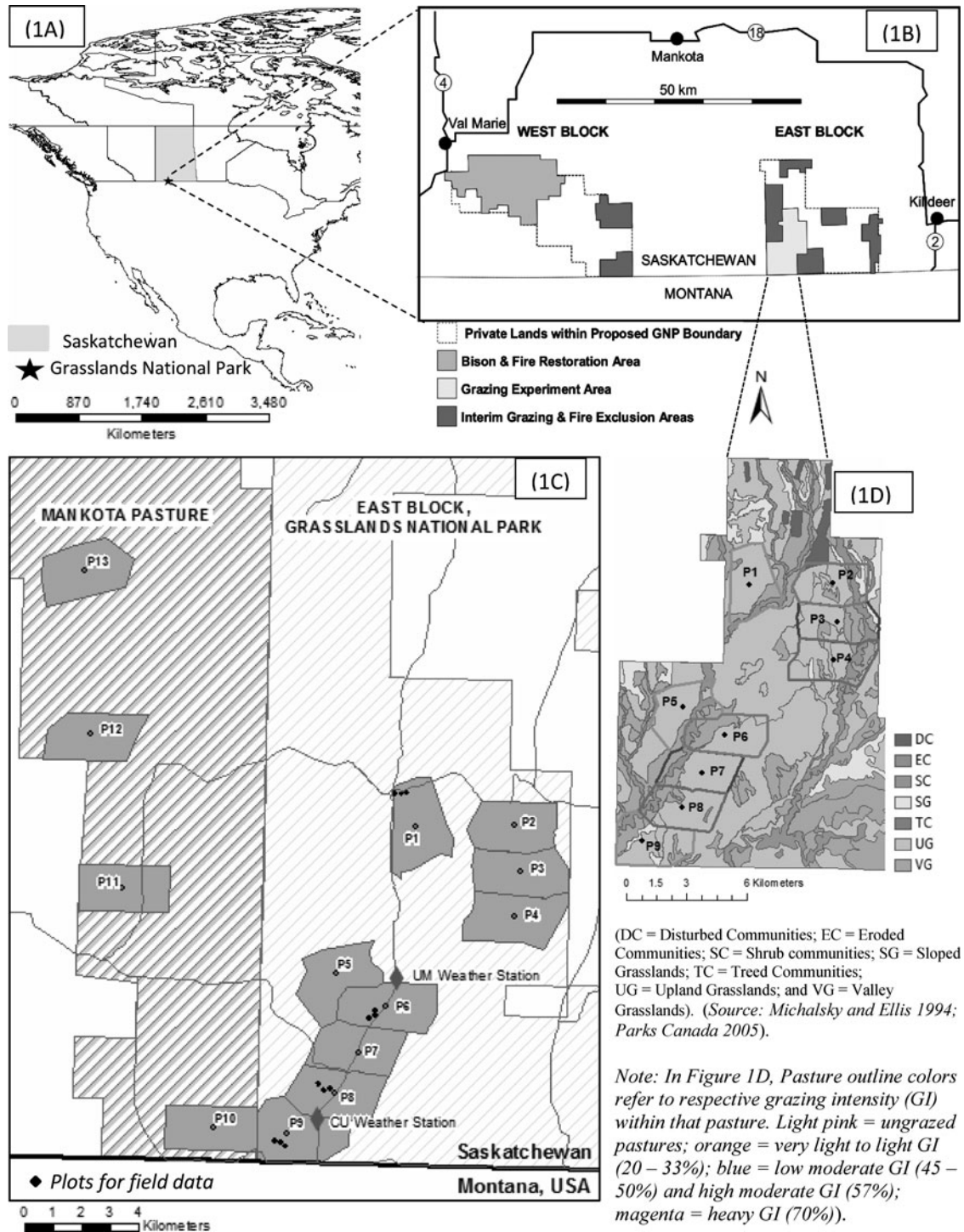
FIG. 1. (A) Location of GNP in North America. (C) Location of experimental pastures in East Block, GNP, and Mankota pasture in Saskatchewan, Canada. (D) Vegetation classification for East Block, GNP.

grazing intensity (P4, P8); P1, P5, and P9 were ungrazed and are considered control pastures in this study). From here through the remainder of the article, grazed pastures will be referred to with respective grazing intensities in subscript: $P2_{20}$, $P6_{33}$, $P7_{45}$, $P10_{50}$, $P11_{50}$, $P12_{50}$, $P13_{50}$, $P3_{57}$, $P4_{70}$ and $P8_{70}$. Ungrazed (UG) pastures will be referred to as $P1_{UG}$, $P5_{UG}$, and $P9_{UG}$.

All the experimental pastures were similar in shape and size, as well as proportion of lowland, riparian, and upland
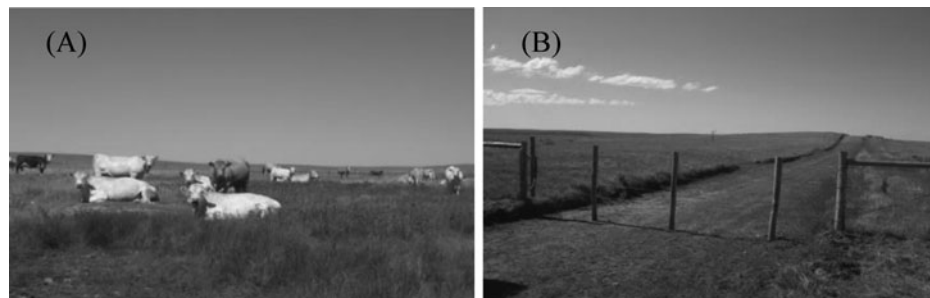
FIG. 2. Biodiversity and grazing experiment photographs for East Block, GNP. (A) Cattle grazing in pasture 3 of East Block, GNP during June 2008. (B) Wire fence between pasture 8 (grazed) and 9 (ungrazed).

habitats, and locations of water and plant communities (Koper et al. 2008). All of the East Block pastures contained several relatively large, permanent creeks, whereas most of the creeks in the Mankota grazed pastures were small and ephemeral. Additionally, to be consistent with the regional pasture management, all the experimental pastures included an anthropogenic water source placed in the lowland areas. To restrict cattle movement, the experimental pastures were wire fenced (Figure 2b).

ALB Estimation

Both destructive and nondestructive methods exist for the estimation of ALB. In general, vegetation clipping to estimate plant productivity is destructive and time consuming (for example, sorting live from dead biomass). Additionally, destructive sampling can be problematic for field studies conducted in conserved or managed areas where management objectives include minimized environmental disturbance. Therefore, to develop relationships between ALB and imagery, field work was conducted combining limited destructive sampling with extensive use of field-based radiometry (also used in a parallel study; only details directly relevant to this paper are reported here). Based on visual survey of the pastures, experimental plots were set up in 2 grazed pastures ($P6_{33}$ and $P8_{70}$) and 2 ungrazed pastures ($P1_{UG}$ and $P9_{UG}$) in the summer of 2008. To capture likely grazing patterns with respect to proximity to water, the experimental plots were positioned between Horse Creek and Wetherall Creek to include upslope (U), midslope (M), and downslope (D) positions. Three experimental plots, each 30 m x 30 m in size, were placed within the selected pastures (Figure 1 and Figure 3). Plot locations were identified using a handheld Global Positioning System (GPS) with a horizontal accuracy of 2 m, and were flagged with a pasture and plot number, using the labeling convention P9U, P9M and P9D (U = upslope, M = midslope, and D = downslope).

A CropScan[1] MSR5 ground radiometer was used to take Normalized Difference Vegetation Index (NDVI) measurements

every meter on each of 4, 30-m transects in each plot (Figure 3 and Table 1).

Within a 30-m transect, ALB measurement was taken every 1 m.

The radiometer was mounted 1.5 m above the ground and had an instantaneous field of view of 28º, giving a spatial resolution of approximately 0.75 m on the ground at nadir. All the radiometer readings were taken within 2 hours of local solar noon. Three readings per point were taken and averaged to smooth out any instrument error. The rationale behind the distance between 2 samples was to capture the local variability of ALB (details of estimation follow). Equally important, however, the experimental plots were a reasonable size to be able to feasibly sample the pastures during the time frame of the study.

Depending on the objective and scale of the research, both ground-based radiometers and satellite imagery have been widely utilized within grassland research to estimate plant biophysical parameters such as ALB (Davidson and Csillag 2001; Flombaum and Sala 2007). Typically, ALB is estimated by establishing an empirical relationship between the destructively measured biomass and the transformations of 2 or more remotely sensed spectral bands. Davidson and Csillag (2001) examined the relationship between numerous spectral vegetation indices and ALB in GNP, Saskatchewan, and found that for their purposes, all the vegetation indices produced similar results. Flynn et al. (2008) concluded that the spatial variability of biomass in pastures and hayfields can be determined accurately using the NDVI measured from a ground-based sensor. Our CropScan measurements comprised reflectance in wavelengths corresponding to Landsat Bands 1–5, meaning a number of vegetation indices were available. Preliminary analysis showing high correlation between the NDVI and the Enhanced Vegetation Index (EVI) ($R^2 = 0.94$, $p < 0.05$), plus Davidson and Csillag's (2001) results, prompted a decision to consider only NDVI for further analysis.

Twelve destructive biomass samples were collected for radiometer calibration purposes at random locations near the experimental transects, followed by biomass clipping in 50 × 10 cm rectangles. All aboveground vegetation was clipped

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[1]CropScan Inc., USA

(A): An example showing Pasture 6 experimental plots (30m x 30m) with transects placed inside and between the plots to capture the spatial variability in soil moisture and productivity.

(B) Photograph showing transects within the Pasture 6 experimental plot.

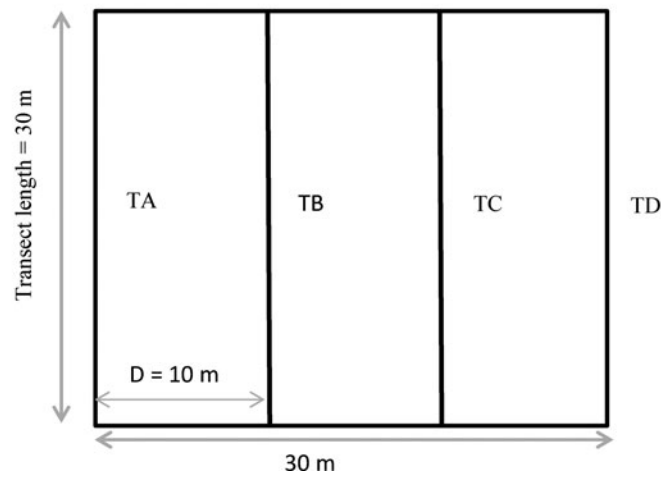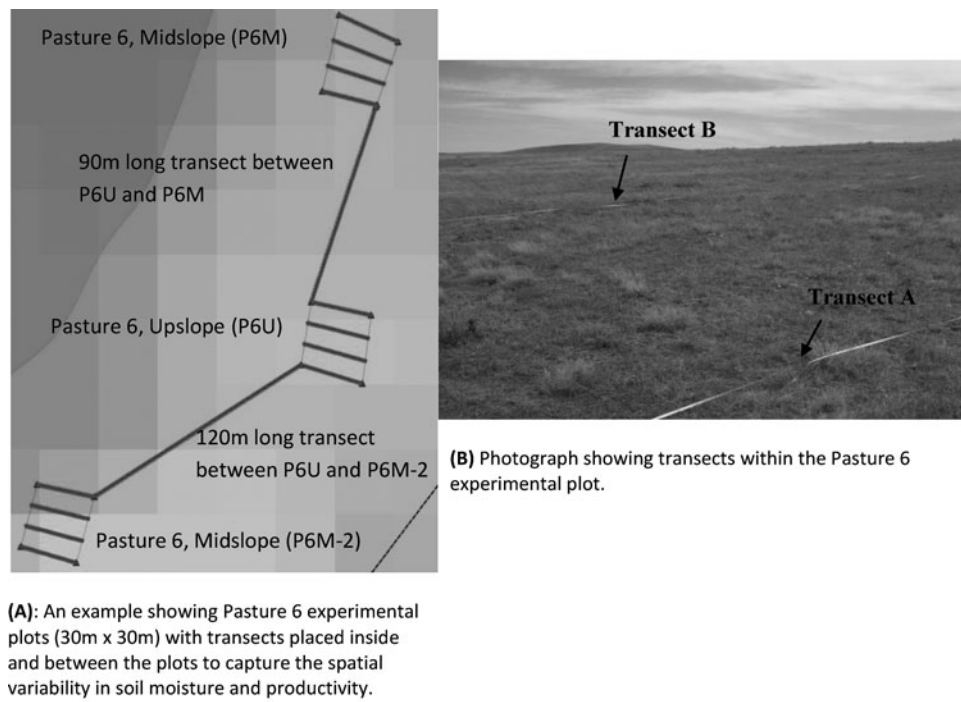

FIG. 3. Experimental Plot (30 m × 30 m) design for ALB Measurements. *Note:* TA = Transect A, TB = Transect B, TC = Transect C, TD = Transect D; D = distance between adjacent transect.

TABLE 1
Summary of number of experimental plots within each pasture and total number of measurements taken per plot

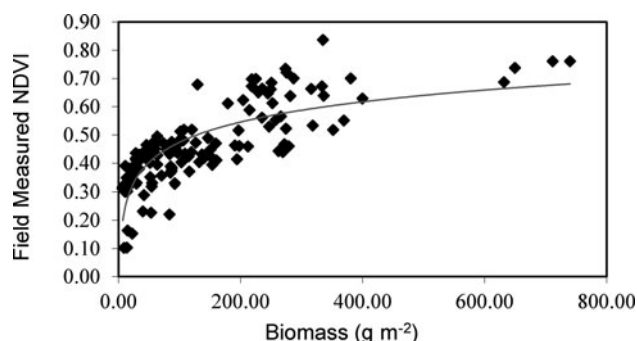| Pasture Number	No. of Plots Within Each Pasture	No. of Transects Within Each Experimental Plot	Total No. of Measurements (SM and ALB) Per Plot
$P1_{UG}$	3	4	124
$P6_{33}$	3	4	124
$P8_{70}$	3	4	124
$P9_{UG}$	3	4	124

FIG. 4. Calibration curve for converting field-measured NDVI to area biomass (g m^{-2}).

using shears and was stored in sealed plastic bags. The vegetation was transported back to the research station and sorted, dried, and weighed within 60 hrs ($\leq$ 36 hours for sorting, for a related project, plus 24 hours oven-drying at 60°C, or until a constant weight was achieved). These data were combined with similar but more extensive field data (vegetation type: grass, selaginella/lichen, forb/shrubs and juniper) collected by Davidson et al. (2006) and Miles (2009) to derive the calibration of Equation (1), used here ($R^2 = 0.61$, $p = 0.000$, N = 130; Figure 4).

$$\text{Biomass} = (5.9803)e^{(5.873 * \text{Field-measured NDVI})} \quad [1]$$

Satellite Data

Previous studies in semiarid regions found Landsat TM data to be very well suited for estimating biomass and cover under different management practices, as well as appropriate for measuring spatial heterogeneity in grasslands (Guo et al. 2000; Zhang et al. 2003). He et al. (2006) suggested that a pixel size of ~35 m would capture most of the spatial variation in biophysical properties of grasslands in this study area (i.e., GNP). Similarly, Davidson and Csillag (2001) determined that resolutions from 10 m–50 m had potential for estimating C_4 species coverage in the GNP area. Therefore, Landsat TM was selected for this study because of its resolution (pixel size approximately 30 m) and availability. Despite better temporal resolution (8 days) than Landsat (16 days), coarser imagery such as Moderate Resolution Imaging Spectroradiometer (MODIS) (250 m and 500 m pixel size) and AVHRR (1.1 km pixel size) were not used, because they would not have been able to detect important spatial patterns below these scales.

The satellite data used in this study consisted of 5 Landsat (TM) scenes (Path/Row: 36/26 and 37/26, as shown in Table 2). Images covering the East Block, GNP, and Mankota community pasture were acquired from the United States Geologic Survey (USGS) Earth Resource Observation and Science Center (EROS)[2] using a maximum 10% cloud cover selection criterion.

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[2]http://glovis.usgs.gov/

TABLE 2
Landsat TM image acquisition information

Landsat Image Acquisition Date	Path/Row
June 30, 2000	37/26
June 27, 2007	36/26
June 29, 2008	36/26
June 23, 2009	37/26
June 26, 2010	37/26

Image Preprocessing

The Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH) algorithm based on MODTRAN 4, within ENVI image processing software[3] was used for atmospheric correction on the Landsat scenes. This algorithm has been tested and shown to be accurate by Mathew et al. (2003) and Davis (2006). The algorithm has the benefit of not requiring any ancillary data other than solar zenith angle and visibility at the time of acquisition, which was acquired from the image metadata. From the standard MODTRAN model atmospheres, mid-latitude summer (MLS) model atmosphere was selected for atmospheric information (e.g., water vapor and surface air temperature). Visibility over the GNP area for each date was obtained from the Environment Canada (2010) website. The FLAASH algorithm was then applied to all bands for all the scenes.

Identification of Grazed and Ungrazed Sites with Variable Grazing Intensity (GI)

Only the portions of each image that were over the study area were analyzed. Vector files that delineated the East Block (GNP) and Mankota community pastures were used to clip the region of interest (ROI) from the Landsat scenes to ensure that other land uses, such as cultivated agriculture, did not impact the results.

Sampling Design for Satellite-Based Data Analyses

Each experimental pasture was analyzed to determine the ALB variability within the pastures. Additionally, transect sampling design was used to see if slope position (upslope and downslope) had any impact on the ALB heterogeneity. Transect length was dependent on the size of the upslope and downslope area within each experimental pasture of the East Block and Mankota community pasture.

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[3]ENVI, 2008; http://www.exelisvis.com/ProductsServices/ENVIProducts.aspx

Weather Data

Plant productivity is affected by various factors, including weather (Knapp et al. 2002). To better understand the interaction between site-specific weather conditions and ALB, an AE50 HOBO Weather Station[4] was installed in $P9_{UG}$. From May 15 to August 21, 2008, it recorded precipitation, temperature, photosynthetically active radiation, relative humidity, wind direction, and speed. Mankota weather station data acquired from Environment Canada (2010) were also used to assess inter- and intraseasonal conditions affecting the ALB.

DATA ANALYSIS AND METHODS

Data were checked for normal distribution using the Kolmogorov–Smirnov test (p-value > 0.05), and were log-transformed where needed to satisfy assumptions of normality and homogeneity of variance. Additionally, data were tested for homoscedasticity using Levene's test (Levene 1960) and Bartlett's test (Snedecor and Cochran 1989).

Mixed effect models—linear mixed effect models (LME) and generalized linear mixed effect models (GLMEs)[5]—were used to separate the fixed effects (i.e., where all levels of an effect are represented) of management (grazing treatment) and slope location from the random effects (i.e., where levels of an effect are assumed random and not fully represented; in this study, this included pasture as a random sampling variable) as in Bell and Grunwald (2004) and Mandle and Ticktin (2012). The year was treated as a fixed effect because treatment could have cumulative effects over time because cattle remove vegetation every season, and the amount and distribution of remaining vegetation in year $n + 1$ depends on the amount of vegetation removed in year n. The rationale for using mixed effects models was their ability to analyze repeated measures data, allowing for sequential sampling from a single plot over multiple dates, and the use of both categorical and continuous effects (variables) simultaneously (Piepho et al. 2003; McCulley et al. 2005). Finally, including random effects in statistical analyses allows us to make inferences beyond the scope of this study, compared to conclusions from fixed effects treatments that can be applied only to differences among those treatments addressed in the study. The temporal data were analyzed using the repeated-measures ANOVA procedure of the SPSS general linear model to estimate the overall significance of treatment effects. When grazing treatment by year interaction or year effects were significant ($p \leq 0.05$), the Tukey–Kramer Honestly Significant Difference (Tukey's HSD) multiple comparisons test (Sasaki et al. 2009) and the Bonferroni corrected test were used to determine which treatment-year combinations and which years differed.

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[4]Onset Computer Corporation, 2007, www.onsetcomp.com/

[5]SPSS version 20.0, IBM Corporation, New York, USA

Geostatistical Analysis Using Semivariograms

Geostatistics handles data sampled in space, allowing the exploration of variability with respect to distance. Most parametric statistics are inadequate to analyze spatially dependent variables because the assumption is that all the measured observations are independent (Cambardella et al. 1994). However, in geostatistics it is assumed that there is spatial autocorrelation (spatial dependence) in the variables, which can be measured and analyzed. Therefore, semivariogram analysis was used in this study to detect the range and spatiotemporal variability in ALB under ungrazed and grazed conditions (e.g., Flynn et al. 2008; Lin et al. 2010). Spatiotemporal changes in satellite-based ALB estimates were quantified using semivariance analyses of 5 Landsat scenes taken June 2000 and June 2007 through 2010. Once experimental semivariograms were calculated, a model was fitted to the semivariogram to assess spatial correlation. Exponential models were used, as this form was found to provide the best fit, with minimum error, and low residual sums of squares (RSS) value (0.00004 to 0.0094). The exponential model is similar to the spherical model in that it approaches the sill gradually, but different in the rate at which the sill is approached and in the fact that the model and the sill never actually converge. The equation used for this model is:

$$\gamma(h) = C_0 + C[1 - \exp(-h/A_0)], \qquad [2]$$

where $\gamma(h) =$ semivariance for interval distance class h, $h =$ lag interval, $C_0 =$ nugget variance ≥ 0, $C =$ structural variance $\geq C_0$, and $A_0 =$ range parameter (Robertson 2008).

Once a variogram model was fit to the data, the parameters, range (A_0), sill ($C_0 + C$, and nugget (C_0) were derived.

Measures of Heterogeneity

Once semivariogram models were derived, 4 derivatives were also calculated to further characterize heterogeneity: correlation ratio (CR), spatial dependence ratio (SDR; or nugget%), magnitude of spatial heterogeneity (MSH), and relative heterogeneity (SH%).

Correlation ratio is the proportion of the nugget effect values to the sill, where values near zero indicate continuity in spatial dependence (Vieira and Gonzalez 2003). It was calculated as:

$$\mathrm{CorrelationRatio} = \frac{\mathrm{NuggetEffect}}{\mathrm{NuggetEffect} + \mathrm{Sill}} \qquad [3]$$

Spatial dependence ratio (SDR) or Nugget% was calculated based on Cambardella et al. 1994.

$$\mathrm{SDR} = \left(\frac{\mathrm{NuggetVariance}}{\mathrm{TotalVariance}}\right) * 100 \qquad [4]$$

This ratio was used to define the spatial dependency classes for soil moisture and ALB. If SDR was (a) $\leq 25\%$, the variable was considered strongly spatial dependent, (b) between 25% and 75%, the variable was considered moderately spatially

dependent, (c) > 75%, the variable was considered weakly spatially dependent (based on Cambardella et al. 1994).

MSH is measured as the proportion of total sample variation accounted for by spatially structured variation (Lin et al. 2010).

$$\text{MSH} = \left(\frac{C}{C_o + C} \right) \quad [5]$$

Spatial variance (C) can be calculated as follows:

$$C = [C_o + C] - C_o \quad [6]$$

Here, is the nugget variance representing random variation (i.e., homogeneity); $C_o + C$ is the sill representing maximum (or total) variation and is spatial variance.

MSH and SH have been widely used to estimate the magnitude of spatial dependence for different soil variables within a site (Robertson et al. 1993; Boerner et al. 1998; Lin et al. 2010). Values for MSH range from 0 to 1, where a value of zero indicates no spatially structured heterogeneity (i.e., samples at all separation distances are independent from each other) and a value of 1 indicates a high amount of spatially structured heterogeneity. Both MSH and spatial dependence are correlated; the higher the MSH, the stronger the spatial dependence.

The proportion of the autocorrelated spatial heterogeneity in the total variation is represented by SH%, which is calculated from the nugget variance and sill (Li and Reynolds 1995):

$$\text{SH}\% = \left(\frac{\text{SillVariance} - \text{NuggetVariance}}{\text{SillVariance}} \right) * 100 \quad [7]$$

Therefore, autocorrelated variation (heterogeneity) can be calculated by subtracting the random variation (nugget) from the total variation (sill).

Similar to MSH, SH% is also positively correlated with the spatial dependence. Similar to the Western et al. (2004) study, correlations were also calculated between the averaged SM and semivariogram variables such as sill, range, and MSH; as well as averaged ALB and semivariogram variables.

Correlograms

Correlograms were also calculated to provide the evidence for the size of the zone of influence and the type of spatial pattern (clustered, dispersed, or random) of the variable under study. The number of observations per distance class and the maximum extent for interpretation of a correlogram varied with the spatial configuration of the 2 sampling designs: transect and grid. The maximum extent of interpretation ranged from 1,200 m for transect, and 1,200 m and 2,400 m for grid design.

RESULTS

Local Weather Variability

Because weather variability has implications for plant growth, Mankota weather station data (Environment Canada
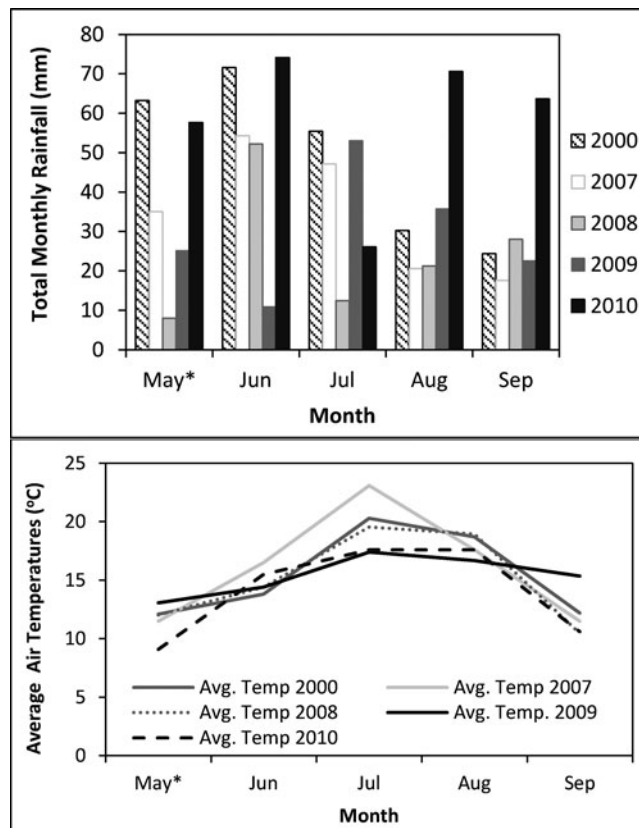

FIG. 5. Total monthly rainfall (mm) and average monthly air temperatures (°C) for growing season in year 2000, 2007, 2008, 2009, and 2010 for the study area.
*Because 2007 precipitation and average air temperature data for May was available only from day 19 onwards, in this graph only days 19 to 31 are presented.

2010) were analyzed to assess inter- and intraseasonal conditions. Total monthly rainfall and average monthly air temperatures for the 2000 and 2007 to 2010 growing seasons are presented in Figure 5. More rainfall was recorded during the 2010 growing season (292.04 mm) compared to all other years (244.80 mm, 174.60 mm, 121.80 mm, and 147.38 mm). June usually received the most rainfall, except in 2009. Timing and amount of rainfall received were also highly variable between years and events. Compared to the other years, 2007 showed higher average air temperatures during June and July.

Effect of Different Grazing Intensities on ALB Spatiotemporal Heterogeneity

There was considerable variability in ALB between low moderate (LM), high moderate (HM), and heavy (H) grazing intensities after 2 years of grazing (Figure 6). Overall, LM had the highest ALB in both 2008 and 2010.

Both grazing intensity (utilization rate) and year significantly affected the ALB (grazing intensity: $F_{(2.2, 894)} = 115.4$, $p <$
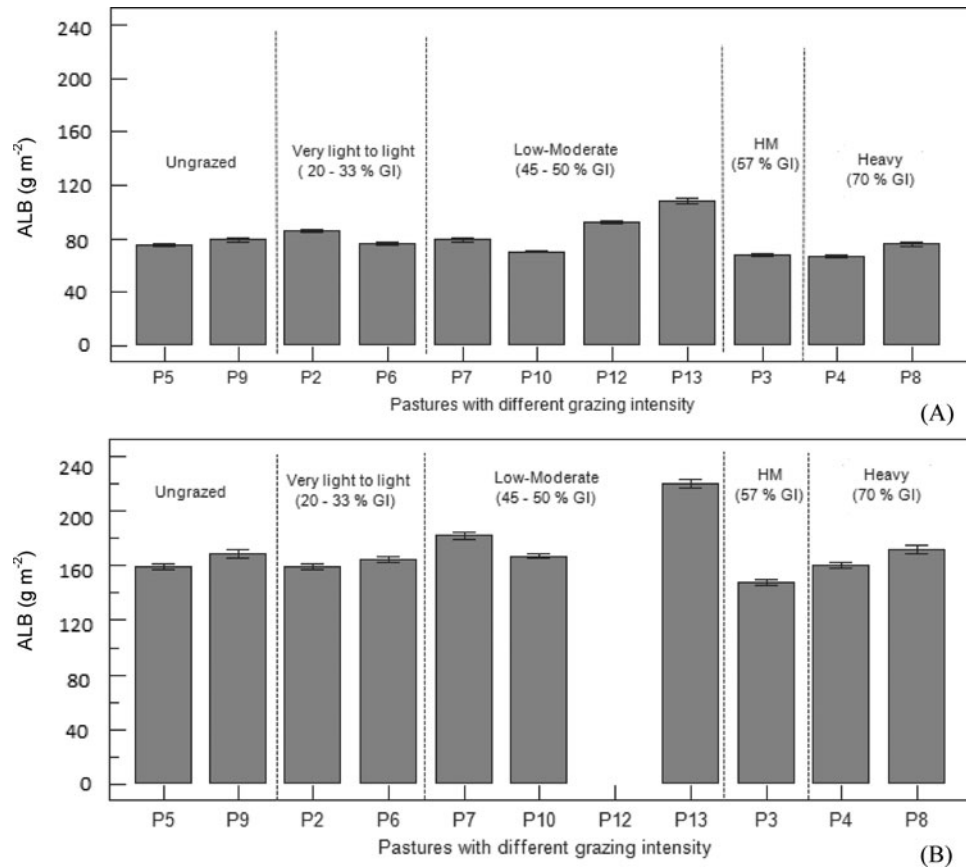
FIG. 6. Spatial variability in ALB among pastures with variable grazing intensity. ALB data is from June 29, 2008 (A) and June 26, 2010 (B). *Note*: P12 data is missing due to cloud cover in the scene. Error bars show 95% CI for mean. No. of observations for each pasture = 3,130.

0.0001; year: $F (2.0, 799.6) = 877.9$, $p < 0.0001$). Approximately 32.5% of the total variance in ALB was accounted for by the variance in year, whereas 68% of the total variance in the ALB was accounted for by variance in the utilization rates.

Main effects of grazing intensity and year were qualified by an interaction of grazing intensity and year ($F (4.2, 1671) = 48.9, p < 0.0001$) with 50.2% of total variance in ALB as a result of grazing intensity (utilization rate) and year. The significant interaction indicated that the magnitude of the grazing intensity effect varied with year.

A Bonferroni-adjusted post hoc test comparing all utilization rates over time showed that mean ALB was significantly ($p < 0.0001$) different between all the grazing utilization rates. Mean ALB was also significantly different before (i.e., year 2007) and after grazing (i.e., year 2008 to 2010) treatment began ($p < 0.0001$). A significant year-by-pasture (with different utilization rates) interaction was also observed ($F (1, 12) = 7.79$; $p < 0.0001$). This secondary effect indicates that although ALB differs annually, it is differentially variable by pasture, suggesting both environmental and grazing intensity influence.

In general, all the pastures showed a moderate-to-strong spatial dependency in ALB, varying from ~1% to ~42% according to the classification of spatial dependency by Cambardella et al. (1994). All experimental pastures (grazed and ungrazed) also showed nugget effect (C_o) suggesting the presence of some local random variation in the dataset (Figure 7). This can be attributed either to measurement errors or to variation prominent at spatial scales smaller than the pixel size, or both ° (Tarnavsky 2008).

The community pastures were examined separately during periods of free range (2000–2007) and controlled grazing (2008–2010). After 7 years of free range grazing, autocorrelated heterogeneity in community pasture P10$_{50}$ increased ~18.2%, whereas in P13$_{50}$, autocorrelated heterogeneity increased only ~4.2% (Figure 8).

In contrast, pasture P12$_{50}$ showed a decrease of ~13% in relative heterogeneity. During the 3 years of controlled grazing, the heterogeneity in ALB increased by ~2.3% in P10$_{50}$, by ~16.2% in P12$_{50}$ and ~11.9% in P13$_{50}$. In comparison, within the park boundaries, the East Block pasture P7$_{45}$, with similar
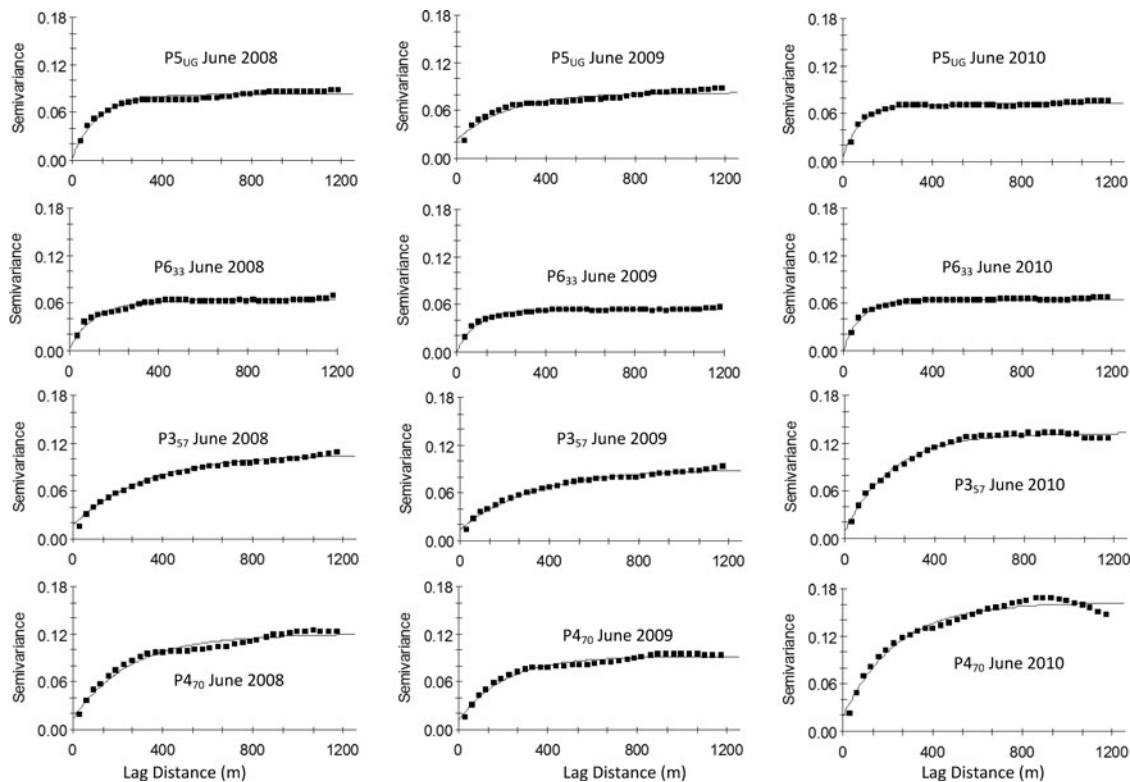
FIG. 7. Semivariograms of ALB in ungrazed (P5$_{UG}$) pasture, pasture P6 with light (P6$_{33}$) grazing intensity (GI), pasture P3 with high-moderate (57%) GI, and pasture P4 with heavy (70%) GI.

grazing intensity, showed a 5.6% increase in ALB heterogeneity after 2 years of grazing.

With the exception noted below, the general pattern was for ungrazed pastures to have the lowest heterogeneity in ALB and a large range of spatial autocorrelation, whereas grazed pastures showed 2.8% to 12.3% increase in heterogeneity (MSH) from 2007 to 2010 and 5.4% to 8.7% increase in heterogeneity (MSH) after 2 years of grazing (2008–2010; Table 3). The exception was the heavily grazed pastures, which showed no change in heterogeneity after 2 years of grazing, suggesting that grazing maintained the existing heterogeneity. Grazed pastures with moderate grazing (low- and high-moderate) showed the most change in heterogeneity after grazing was introduced (2007–2010, change in MSH = 12.3% for LM and 7.1% for HM; 2008–2010, change in MSH = 7.0% for LM and 8.7% for HM). Although all the grazed pastures showed higher heterogeneity values for ALB compared to ungrazed, grazed pastures with very light to light grazing intensity had the highest MSH value after 2 years of grazing (0.998) followed by low-moderate (0.957). Overall, the range for ALB over time decreased for all the grazing intensities, suggesting that vegetation patch size is negatively affected by grazing activity (Figure 9).

Similar to Lin et al. (2010), range and MSH were compared among grazing intensities by one-way ANOVA and regression analysis to determine whether or not grazing intensity (utiliza-

tion rate) was a significant predictor for the geostatistical metrics. Out of all the regression models, exponential and inverse models were found to be the best options representing the MSH and range data to show the trend over time. After cattle were allowed to graze for 2 years at different intensities, a decrease in patch size (range) for ALB was observed corresponding to grazing intensity (exponential model, 2008: $\beta = -0.959$, $t = -5.857$, $p = 0.009$, $R^2 = 0.92$; 2009: $\beta = -0.959$, $t = -5.901$, $p = 0.009$, $R^2 = 0.92$; 2010: $\beta = -0.959$, $t = -5.832$, $p = 0.01$, $R^2 = 0.92$).

An increase in MSH for ALB was observed after 2 years of grazing corresponding to grazing intensity (inverse and exponential model, 2008: $\beta = -0.922$, $t = -4.13$, $p = 0.026$, $R^2 = 0.85$; 2009: $\beta = -0.952$, $t = -5.432$, $p = 0.01$, $R^2 = 0.90$; 2010: $\beta = -0.974$, $t = -7.45$, $p = 0.005$, $R^2 = 0.95$). All the grazed pastures showed higher MSH than the ungrazed pastures (the proportion of total sample variation accounted for by spatially structured variation increased over time with the grazing pressure).

When correlograms were constructed, the number of observations per distance class and the maximum extent for interpretation varied with the spatial configuration of the 2 sampling designs. The maximum extent of interpretation ranged from 1,200 m for transect, and 1,200 m and 2,400 m for grid design (Figure 10). Transect sampling design (using sample points
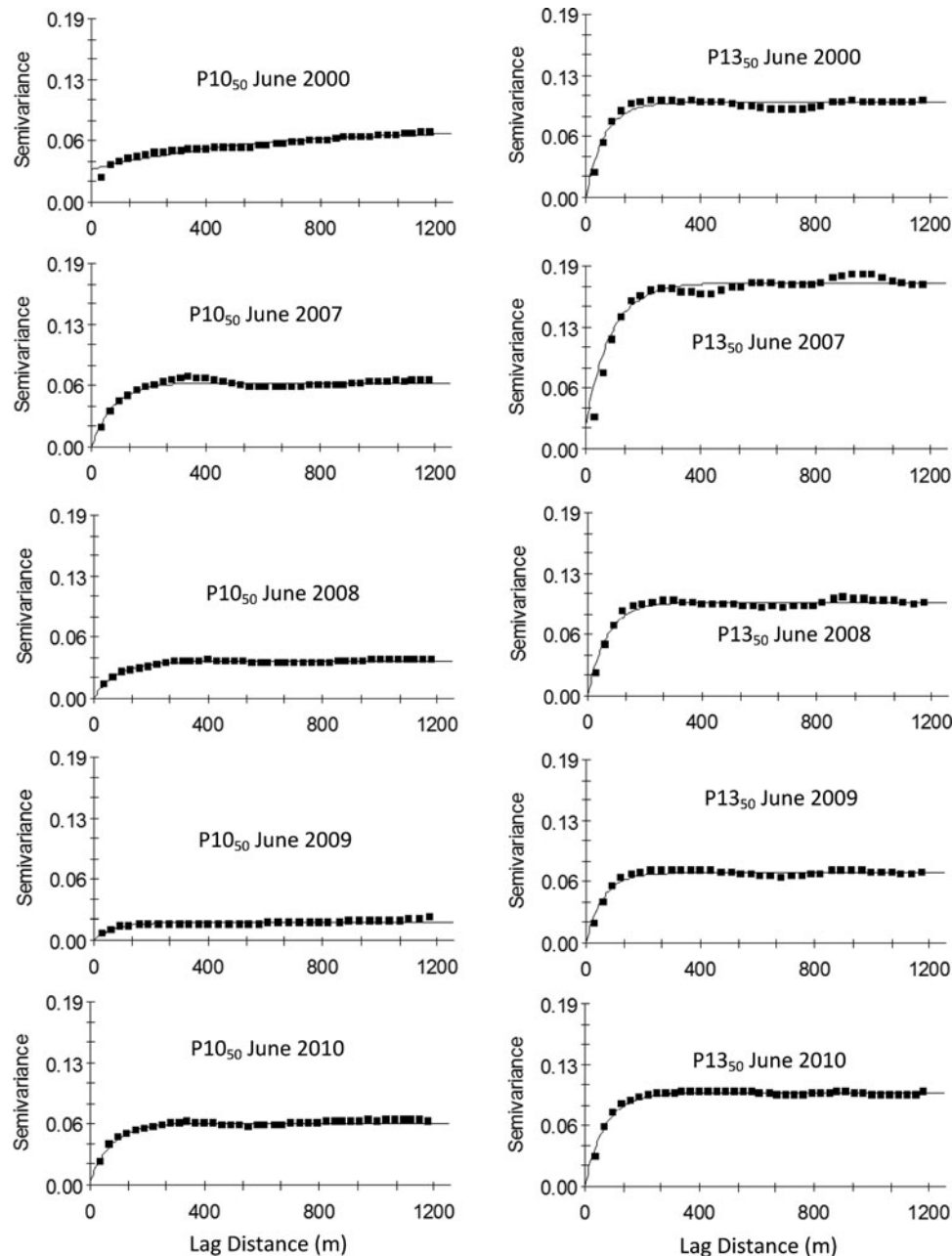
FIG. 8. Semivariograms of ALB in low-moderate grazing intensity (50%) pastures 10 (P10$_{50}$) and 13 (P13$_{50}$) located in Mankota community pasture. *Note*: Semivariograms for years 2000 and 2007 represent pastures with free range grazing, whereas semivariograms for years 2008 to 2010 represent pastures with controlled low-moderate grazing.

along transect placed within a pasture) exhibited a wavelike pattern within the experimental pastures. For example, in the P2$_{20}$ correlogram, the first change of sign from positive to negative value occurred around 60 m, which corresponded to the spatial range of the patches.

The correlogram showed some repetitive patterns of patches; however, both the patch size and the distances among the patches were quite variable. Similarly, other experimental pastures such as P3$_{57}$, P8$_{70}$ (Figure 10), and P13$_{50}$ also showed patchy spatial pattern with variable patch size and distance among the patches. In comparison, P2$_{20}$'s spatial correlogram based on the grid sampling design (1,200 m extent) showed a gradient spatial pattern with significant positive values at short distances to negative values at large distances. However, it leveled at

TABLE 3
Summarized sill, range, and MSH results for different grazing intensities for years 2007, 2008, and 2010

Year	GI	Sill ($C + C_o$)	Range (m)	MSH (C / [C + C_o])
2007 (No grazing)	UG	0.180	1,348	0.690
	VLL_{BG}	0.143	324	0.970
	LM_{BG}	0.124	315.2	0.834
	HM_{BG}	0.212	257	0.894
	H_{BG}	0.239	172	0.938
2008 (Start of grazing)	UG	0.122	1,294	0.658
	VLL_{AG}	0.075	249	0.944
	LM_{AG}	0.075	293	0.887
	HM_{AG}	0.107	324	0.838
	H_{AG}	0.128	188	0.942
2010 (after 2 years of grazing)	UG	0.099	1,353	0.652
	VLL_{AG}	0.063	180	0.998
	LM_{AG}	0.095	236	0.957
	HM_{AG}	0.133	212	0.925
	H_{AG}	0.153	180	0.941

Note: GI = grazing intensity; BG = before grazing; AG = after grazing; UG = ungrazed; VLL = very light to light grazing (20%–33% GI); LM = low-moderate grazing (45%–50% GI); HM = high-moderate grazing (57% GI); and H = heavy grazing (70% GI); MSH = magnitude of spatial heterogeneity.

around zero, indicating absence or nondetection of spatial patterns at distances > 220 m. Similarly, pastures P3$_{57}$, P8$_{70}$, and P13$_{50}$ showed positive values at short distances with significant spatial autocorrelation. P3$_{57}$ and P8$_{70}$ also showed alternation of values from positive to negative, thus indicating patchiness. Correlations for P13$_{50}$ oscillated along the zero value suggesting absence of any significant spatial autocorrelation at large distances. The spatial range (zone of influence, patch size) for pasture P13$_{50}$ was around 360 m, a distance at which the sign of the values changed from positive to negative.

Overall, correlograms based on either of 2 sampling designs were globally significant, indicating that the overall spatial pattern of ALB is not random, but it is likely that there are spatial patterns existing at smaller distances than the distances between sampling pixels, which could not be detected by the grid sampling design (Wiens 1989). Smooth curves displayed by the grid sampling design compared to transect design are due to averaging over several directions. The patterns are clearer for grid sampling design when correlograms were calculated for 2,400 m extent.

A significant effect of grazing intensity on ALB was found even after controlling for the effect of slope position (F (4, 943) = 12.74, $p < 0.001$; N = 953). Post hoc test (Tukey's HSD) results indicated that mean ALB values were significantly different ($p < 0.001$) between the upslope and downslope locations for all the grazing intensities, where downslope areas showed higher mean ALB values than upslope areas.
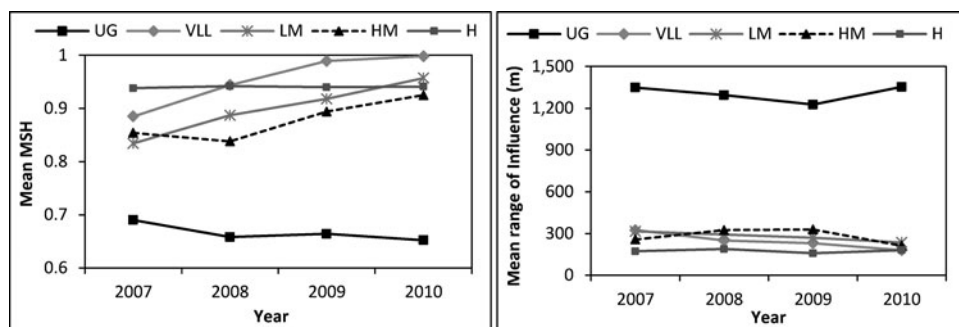

FIG. 9. Comparison of mean MSH and mean range of influence between different grazing intensities for no grazing (year 2007), at the start of the grazing (year 2008), after 1 year of grazing (year 2009), and after 2 years of grazing (year 2010).
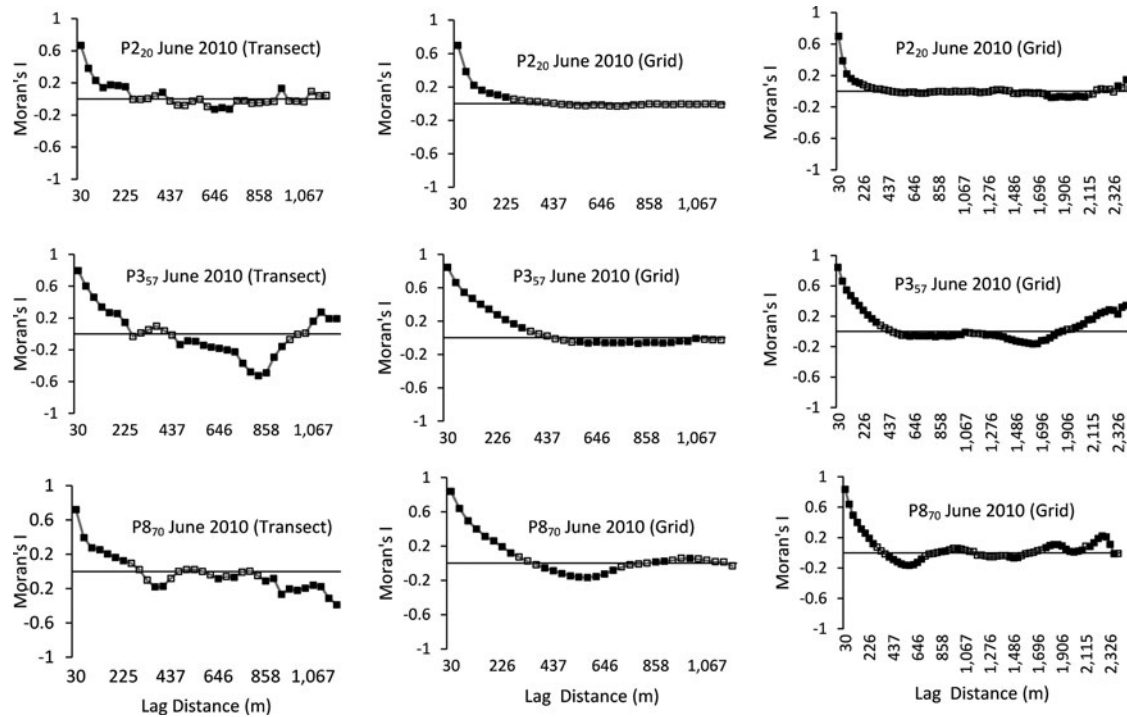
FIG. 10. Effect of grazing intensity and sampling design (Grid vs. Transect) on the ALB spatial pattern (Moran's I): An example of VLL (P2$_{20}$), HM (P3$_{57}$), and heavy grazing (P8$_{70}$) is provided. (Lag distance = 1200 m for Transect and Grid; 2400 m for Grid only, lag class distance interval = 30 m). *Note*: P2$_{20}$ = pasture 2 with very light to light (20%) grazing intensity (GI); P3$_{57}$ = pasture 3 with high-moderate (57%) GI; P8$_{70}$ = pasture 8 with heavy (70%) GI. Solid squares indicate significant coefficient values at $\alpha = 0.05$; open squares indicate nonsignificant coefficient values after progressive Bonferroni correction.

DISCUSSION

Spatial Heterogeneity in Grazed and Ungrazed Pastures

All the grazed pastures showed variability in ALB over the years (Figure 6). Despite the variability in ALB, overall grazed pastures showed higher ALB than ungrazed pastures, where ALB was greatest in the moderately grazed pastures with 50% grazing intensity. The findings were consistent with Holecheck et al. (2006) and Jamiyansharav et al. (2011), which also showed higher biomass production in the moderately grazed pastures than in the ungrazed sites.

NDVI and, therefore, the estimated ALB (g m^{-2}) values increased and decreased over the years within grazed and ungrazed pastures, which is common in semiarid grasslands (Milchunas et al. 1994). This is because temporal (seasonal and interannual) variability in plant processes is largely a function of changes in soil temperature and moisture over time (Epstein et al. 2002; Knapp et al. 2002). Due to satellite data limitations and imagery quality at the desired scale, it was not possible to separate the effect of interannual variation on the mean ALB values in the grazed pastures. This is because desired image quality (< 10% cloud cover and shadows) for the study area limited the scene acquisition to single dates in 1 or 2 months of the growing season, for example, June 29, 2008, June 23, 2009, and

June 26, 2010. This resulted in insufficient data samples to run the correlation analysis to determine the impact of both rainfall and grazing intensity on ALB variability. Therefore, to differentiate rainfall-induced fluctuations from changes in vegetation dynamics caused by different grazing intensities, monitoring must include seasonal data and/or interannual data for long periods in order to have adequate sample size.

The study area showed variation in the weather conditions over a 4-year study period. Both timing and amount of rainfall received were highly variable between the years and events (Figure 5). A study conducted by Fay et al. (2000), for a mesic grassland ecosystem located in northeastern Kansas, identified rainfall interval as the primary influence on the soil and plant responses, with increased intervals causing reduction in total aboveground net primary productivity (ANPP) and flowering duration. This is because increased intervals between rainfall events can create soil water deficits, thus affecting the available water for plant growth.

A significant linear correlation was found between the amount of biomass available for grazing and grazing intensity ($R^2 = 0.862$, $p < 0.0001$), where, in general, ALB increased with grazing intensity. Wallace and Crosthwaite (2005) also reported a significant linear correlation between biomass and grazing intensity ($R^2 = 0.365$, $p < 0.0001$). However, ALB for

57% and 70% grazing intensity was lower compared to VLL and LM grazing intensities.

The semivariogram analysis showed higher spatial heterogeneity in ALB for grazed pastures with variable utilization rates than ungrazed pastures (Table 3). A study by Johnson et al. (2011) on grazing intensity effects on grassland birds also showed increased heterogeneity over time with increase in grazing intensity. In this study, heavily grazed pastures showed the highest ALB heterogeneity in 2007 (no grazing year) compared to other pastures. However, after the introduction of grazing in year 2008, higher heterogeneity in ALB over time was observed in VLL and LM pastures than heavily grazed pastures, indicating a quadratic effect (Figure 9). Similarly, Lin et al. (2010) reported a quadratic relationship between the ALB heterogeneity and stocking rates. Overall, grazed pastures showed increased heterogeneity after 2 years of grazing with high-moderate grazing, showing the highest change in heterogeneity under low-moderate grazing intensity. An exception was heavily grazed pastures, which showed no change in heterogeneity after 2 years of grazing, suggesting that grazing maintained the heterogeneity over the years. It is likely that forage availability remained high enough, even under the highest utilization rate, that cattle did not have to utilize previously ungrazed patches during the grazing period, which most likely would have homogenized the vegetation structure to some degree. Similar studies of the effects of grazing intensity on spatial heterogeneity of vegetation have documented changes (increase or decrease) in spatial heterogeneity over time, where study results are likely affected by the vegetation utilization level, response variable, and spatial scale evaluated (Townsend and Fuhlendorf 2010). Because the management goals for the GNP include increasing species heterogeneity as essential to maintaining and sustaining biodiversity within the GNP, 70% grazing intensity may be too high. However, other studies document the association of some rare native plants (example, blowout penstemon, *Penstemon haydenii*) and animals (such as the black-footed ferret and mountain plover) with heavily grazed areas (Klute et al. 1997; Stubbendieck et al. 1997). Therefore, if economically possible, a range of grazing intensities (low-moderate-heavy) will be more suitable for the GNP in providing habitats for a greater suite of species preferring variable vegetation cover than incorporating limited ranges of grazing intensities (low and moderate).

Based on personal observation during the field work conducted in summer 2008, soil characteristics, vegetation type (grass, shrubs, forbs, and other) within the lowland, upland, and riparian areas of each pasture, and cover (sparse, dense, bare, or mixed) was highly variable among the experimental pastures. This is likely the cause of variation in addition to local weather variation within the ungrazed pastures (Vallentine 2001; Harrison et al. 2003). In comparison, grazing activity is an influencing factor for the variability in ALB in the grazed pastures. For example, compaction due to grazers can alter the soil structure, which may change the soil aeration and moisture retention capacity, affecting the plant available water (Jacobs et al.

2004). Any change in plant available water will further impact the plant growth as well as plant productivity, thus contributing to more variability between the grazed and ungrazed pastures. In short, grazing disturbance can help create and maintain the heterogeneity in ALB, which is crucial for the successful coexistence of many grassland species (Fuhlendorf and Engle 2004; Vermeire et al. 2004).

Effects of Grazing Intensity and Slope Location on ALB

Grazing intensity (utilization rates) and year significantly influenced the spatial variability in ALB ($p < 0.0001$). The mean ALB values were also significantly different among the grazing intensities ($p < 0.05$). Overall, the reduction of ALB by intensive grazing (high-moderate to heavy) also led to the decline of range for ALB, suggesting that vegetation patch size decreased with grazing pressure. This supports a view of grazing as a characteristically patchy process (Adler et al. 2001), where patchiness could be due to plant defoliation, trampling, and excretion during the grazing period (Damhoureyeh and Hartnett 1997). For example, grazers' excretory products are nutrient rich, which creates patches with elevated nutrients readily available for plants. These nutrient-rich patches generally have altered plant species composition (Steinauer and Collins 2001). Also, some studies show that grazers often "patch graze" by preferentially grazing some areas repeatedly while leaving other areas ungrazed until forage availability is low (Coghenour 1991; Cid and Brizuela 1998). As a result of this preferential grazing, patchiness is either maintained or enhanced in time.

In addition, field pictures from summer 2008 in the East Block of the GNP showed a high amount of variability in the type of vegetation within all the experimental pastures. For example, P8$_{70}$ showed presence of poisonous grass death camas (*Zigadenus venenosus*), which is avoided by the grazers. This may have also contributed to patchy patterns within the experimental pasture. Additionally, vegetation patches with cow patties and urine are generally avoided by the cattle in the same year (Steinauer and Collins 2001), which could have also added to patchiness. Such patchy grazing tends to enhance biodiversity (Fuhlendorf and Engle 2004; Truett et al. 2001).

Cattle selectivity based on plant palatability and nutritive quality is likely one of the contributing factors for the patchy vegetation patterns. Generally, the nutritive quality of forage declines as the growing season progresses, which affects the cattle foraging decisions. This is because cool-season grasses (C_3) have higher nutritive quality early in the season compared to warm-season grasses (C_4) that grow later in the season (Adams et al. 1996). Additionally, variation in grazing intensity with light grazing in some areas and heavy grazing in others also results in a mosaic of vegetation types, thereby influencing not only the plant community but diversity in animals and insects as well (Hartnett et al. 1996; Knapp et al. 1999).

There was a significant effect of grazing intensity on ALB even after controlling for the effect of slope position, and mean

ALB values were significantly higher downslope. Plant community composition is notably different between the upslope and downslope areas, which may have led to some of the observed structural differences. Artificial water supplies and salt cubes were provided in uplands to encourage forage utilization in these areas and to reduce cattle damage to riparian areas. This also could have influenced the grazing patterns in the pastures, because water availability is an important factor in cattle foraging decisions (Briske et al. 2008). Studies such as Adler et al. (2001), Vallentine (2001), and Bradley and O'Sullivan (2011) concluded that factors such as slope, quality or desirability of forage, and distance to water influence the grazing distribution.

Spatial Patterns of ALB over Time

Two sampling designs, grid and transect, were used to determine the spatial patterns in ALB with specific focus on smoothness of the correlogram. In our study, both designs were able to detect the spatial patterns in ALB. However, a grid design provided smoother correlograms as a result of more numbers of pairs per distance class than transect sampling design for the same maximum distance.

Although coefficient of variance (CV; the standard deviation of a variable divided by its mean) measurements can provide an indication of the magnitude of variance, geostatistical analysis is needed to quantify different aspects of the spatial heterogeneity, including the degree and range of autocorrelation (Li and Reynolds 1995). All the spatial correlograms showed the strongest value of spatial autocorrelation within the first distance class and corresponded to the spatial range of the patches. For a separation distance > 440 m and < 1,200 m, spatial autocorrelation of ALB was generally neutral to slightly negative. Spatial autocorrelation of ALB in high-moderate and heavily grazed pastures was consistently close to zero at intermediate separation distances, indicating some random variation. The lack of spatial structure at intermediate distances might be indicative of random arrangement of patches created as a result of grazing disturbance (Cid and Brizuela 1998).

The spatial correlograms for the grazed experimental pastures based on transect sampling design exhibited a wavelike pattern compared to correlograms based on grid sampling design at the same maximum distance (1,200 m). The patchy pattern observed in both sampling designs is most likely caused by selective grazing by cattle, trampling, and waste deposition, which provide sites for plant germination as a result of high nutrient availability (Sternberg et al. 2000). Overall, the correlograms from both sampling designs showed some repetitive pattern of patches; however, both the patch size and the distances among the patches were quite variable.

CONCLUSIONS

The results from this study contribute to a developing body of literature that suggests that the effects of livestock grazing on the spatial heterogeneity of vegetation is variable depending on the grazing intensity, response variable, and spatial scale evaluated. Overall, observations show that low-to-moderate grazing intensity increases ALB heterogeneity over time, whereas no change in ALB heterogeneity over time was observed for heavy grazing intensity. As expected, all grazing intensities caused decrease in semivariogram range (patch size) over time, confirming that grazing is a patchy process. This study demonstrates that cattle grazing with variable intensity both maintained and changed the spatial patterns of ALB in the studied mixed-grassland ecosystem because of the selective nature of the cattle. This information can be used in the development of effective grazing system designs to maintain heterogeneity and restore biodiversity in grassland ecosystems, which is one of the main goals of Parks Canada. Furthermore, to achieve production and conservation objectives, many federal, provincial/state, and local organizations within North America implement grazing practices for which one needs to consider heterogeneity as well as evaluate the ecosystem responses to grazing intensities at spatial extents (pasture size 300 ha or larger) relevant for range managers.

We identify several future directions of research that could further develop or refine these conclusions. First, we recommend that future studies should assess the impact of distance from watering points on the vegetation spatial patterns under different grazing intensities. This will help with better understanding of the impact of grazing intensity on overall heterogeneity. Questions about weather variability and its impact on production are also important for looking at temporal variability of effects of grazing intensity on ALB heterogeneity. Because grasslands have developed under the influence of frequent and extensive fires and intensive grazing, both these disturbances are required for proper maintenance of grasslands (Coupland 1991; Hartnett et al. 1996; Fuhlendorf and Engle 2004; Vermeire et al. 2004). Future grazing studies should incorporate the interactions of these disturbances on the ALB heterogeneity. Patch burning within a pasture is suggested as this will allow cattle to access both burned and unburned vegetation during subsequent growing seasons.

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