

Precipitation timing and grazer performance in a tallgrass prairie

Joseph M. Craine, E. Gene Towne, Doug Tolleson and Jesse B. Nippert

J. M. Craine (jcraine@ksu.edu), E. G. Towne and J. B. Nippert, Div. of Biology, Kansas State Univ., Manhattan, KS 66502, USA. – D. Tolleson, School of Natural Resources, Univ. of Arizona, Cottonwood, AZ 86326, USA.

Changes in precipitation amount and variability have the potential to alter the structure and function of grasslands, but we know little about how changes in the timing of precipitation might affect grasslands. Here, we analyze long-term records from a tallgrass prairie to show that shifts in the timing of precipitation during the growing season have little effect on primary productivity or grass reproduction, but can greatly affect grazer performance. While greater late-season precipitation increases the weight gain of adult and young bison, greater mid-season precipitation decreases their weight gain. In addition, calving rates are lower after years with greater mid-season precipitation and higher after years with greater late-season precipitation. As well-timed drought can actually increase grazer weight gain and reproduction, it will be necessary to generate predictions of within-season distribution of precipitation to successfully forecast future grazer performance.

An integrated understanding of how ecosystems will respond to future climatic variability will require understanding responses to both the degree and timing of precipitation variability as changes in precipitation have the potential to alter the structure and function of grasslands and their ability to provide ecosystem services. Investigations into the effects of changes in precipitation on grassland dynamics have largely focused on changes in the total growing-season precipitation (Knapp and Smith 2001, Bai et al. 2004, Huxman et al. 2004) or precipitation variability – namely differences in the size and distribution of precipitation events (Knapp et al. 2002, 2008, Weltzin et al. 2003, Reynolds et al. 2004, Nippert et al. 2006, Swemmer et al. 2007, Robertson et al. 2009, Volder et al. 2010).

Beyond changes in total precipitation and variability in event size, ecosystem response to climate variability that occurs on the scale of weeks to months depends on the time of year of the variability (Pitt and Heady 1978, Hanson et al. 2005, Knapp et al. 2006, Craine et al. 2009, 2010a, Ma et al. 2010, De Boeck et al. 2011, La Pierre et al. 2011). Yet, we still know too little about how the timing of short-duration climate variability on these scales impacts basic ecosystem processes such as primary production. Beyond our lack of understanding of how variability in the timing of precipitation affects primary productivity, we know little about the potential consequences of changes in the timing of precipitation within the growing season and how these changes might affect grazers. For example, the abundance and performance of grazers varies along precipitation gradients (East 1984, Fritz and Duncan 1994) and has been linked to interannual variation in climate (Toigo et al. 2006, Martinez-Jauregui et al. 2009, Hamel et al. 2010).

Yet, how changes in the timing of precipitation during the growing season might affect grazers in a given grassland is unknown since grazer performance also depends on grass nutritional quality – the concentrations of available energy and protein in plant tissues (Breman and de Wit 1983, Van Soest 1994, Coté and Festa-Bianchet 2001, Craine et al. 2009).

Previous research showed that juvenile bison in the tallgrass region of North America responded differently to variation in precipitation midsummer vs late-summer (Craine et al. 2009). Yet, as juvenile bison are supplemented nutritionally from their mothers for up to two years, it is uncertain whether the differential responses to precipitation at different times of year would extend to adult bison or impact reproduction, which likely would have a larger impact on population dynamics than weight gain per se. In addition, it has previously been shown that the reproduction of different grass species responds differently to precipitation at different times of year (Craine et al. 2010a), but it is still an open question as to what the critical climate periods are for grass production no less whether climate effects that are manifested through grass quality respond quickly to variation in climate or are delayed to later in the growing season.

To better understand how variation in climate within a growing season affects bison growth and reproduction, we use critical climate period analysis (Craine et al. 2009) to test the effects of precipitation at different times during the growing season on processes for a North American tallgrass prairie, Konza Prairie. Using long-term annual measurements of bison *Bison bison* weights and reproduction, we focus on understanding the relative importance of the

amount and timing of precipitation for the performance of this keystone grazer as well as for the biomass production and reproduction of the grass it eats. More specifically, the major goals of the research presented here are to better understand 1) whether critical climate periods for weight gain of adult bison of both sexes match juvenile bison, 2) whether the timing of climate variability that affects weight gain also affects reproduction, and 3) whether the periods for when climate variability impact bison performance are similar to those that impact grass production and flowering.

Methods

Site description

At Konza, 30 bison were introduced into a 450 ha unit in 1987. The area accessible to bison increased in 1992 to 961 ha spread across 10 watersheds. Within the bison unit, two watersheds have been burned in the spring since 1988 at each of three fire frequencies (1, 2 and 20 years), while four watersheds have been burned every four years. The dominant grasses at Konza include *Andropogon gerardii*, *Sorghastrum nutans* and *Schizachyrium scoparium*. Animals feed on natural vegetation available to them at the site and are not supplemented with protein or energy except when held in the corral for short periods before weighing. Since 2000, female calves have received calthood vaccinations and all animals have received injections to control parasites. At this time, most two-year animals are permanently removed from the herd as well as males older than seven years and females that are either 15 years old and barren or have not calved in the previous two years. The sex ratio of mature females to males is maintained at approximately 5:1. After an average of three days in the corrals, remaining animals are released back into the bison unit.

Weight and calving data

Bison are collected into a single corral each November, each individual weighed on a electronic chute scale, and calves are fitted with a uniquely-numbered ear tag. Data for adult female and male weights were restricted to individuals that were 3.5 years and older at the time of weighing. Most males are removed from the herd at the age of 2.5 years, with heavier males more likely to be maintained in the herd. Hence, including changes in weight gain for males between 2.5 and 3.5 years would bias the analyses of weight gain if the data were included. Most females do not typically give birth until three years, which better allows for comparisons of reproductively mature animals. For both adult males and females, weights from 2000–2010 are analyzed. Data on reproductive status of females were not collected before 2000 and there were too few adult males that were weighed annually before 2000 for robust comparisons. Weights were analyzed only if the age of the animal was known.

For calves and yearlings, we analyzed weight data from 1994–2010 and 1995–2010, respectively. Our analyses on calf and yearling weights build on previous analyses (Craine

et al. 2009), which had used weights measured through 2007. Calving rates from 1994–2010 are based on the ratio of the number of calves present at the fall survey and the number of adult females greater than 2.5 years of age. In most years, approximately 2–5 adult females were known to have given birth to a calf each year, but the calf perished prior to the fall survey. These females were not considered as having had a calf.

ANPP and flowering data

Flowering data consists of mass of culms produced per unit area of the three most abundant grasses (*Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans*). The flowering responses of the three grass species were measured at the end of the growing season (after late September) from 1984–2010 along four permanent transects on both the upland and lowland topographic positions in an annually-burned ungrazed watershed (watershed 1D). Along each transect, all flowering culms that occurred in six randomly spaced 0.25-m² quadrats were counted ($n = 24$ plots per topographic position). The flowering culms of each grass species in the plot were then harvested at ground level, dried at 60°C for 2–3 days, and weighed. Our current analysis is similar to previous analyses, which had been through 2008 (Craine et al. 2010a), except that for simplicity we average culm biomass between the two topographic positions rather than present data on uplands and lowlands separately.

Graminoid ANPP was measured at the end of each growing season from 1984–2008 by clipping all vegetation in five randomly selected quadrats (20 × 50 cm) adjacent to the flowering transects ($n = 20$ quadrats in each landscape position each year) in the annually-burned, ungrazed watershed. Biomass was clipped to ground level, separated into graminoid, forb, and woody components and dried at 60°C before weighing. Graminoid ANPP included live biomass as well as current year's dead, which was measured separately from live biomass for 19 of the 25 years. Critical climate periods for graminoid ANPP had not been previously determined, though see Craine et al. (2012).

Fecal collections

To predict dietary crude protein (CP) and digestible organic matter (DOM), fresh fecal material was collected from an average of five adult females approximately biweekly during the growing season and monthly from November–March. We used near infrared spectroscopy of fecal material from adult females to periodically estimate CP and DOM in 2009 and 2010 based on calibrations generated from cattle. The technique is currently most applicable for bison when forage quality is above maintenance levels (approximately 70 mg g⁻¹ crude protein or DOM:CP < 10 for non-lactating animals) (Subcommittee on Beef Cattle Nutrition-Committee on Animal Nutrition - National Research Council 2000) and is likely less able to resolve variation for bison at or below these levels (Plumb and Dodd 1993).

Fecal samples were frozen and later dried at 60°C in a forced air oven, ground to 1 mm particle size and re-dried at 60°C prior to scanning with near infrared spectroscopy

(NIRS) by the Grazingland Animal Nutrition Lab (GAN Lab) (Lyons and Stuth 1992, Roberts et al. 2004). Spectra (400–2500 nm) were collected on a scanning monochromator with spinning cup attachment. Reference chemistry and chemometrics for NIRS calibration development that link forage chemistry and fecal spectra were generated for cattle as described by Showers et al. (2006).

Statistical analyses

In analyzing weight data, both calf weight and yearling weight gain were averaged each year by sex. To determine standardized adult female weights for each year, least squares regression of weight was run that included the identity of the year, the weight of the individual the previous year, animal age, and whether the female had a calf the year before. A similar model was run for adult males and juveniles that included the age of the animal and the weight of the animal the previous year.

Critical precipitation periods for grass ANPP, culm production, bison weights, and calving rates were identified by varying the start and end dates of the precipitation periods to maximize explained variation in weights for the two age classes simultaneously (Craine et al. 2009, 2010a). At each site and each year, total precipitation was determined for 609 periods using precipitation data from a weather station located close to the Konza headquarters (ATP01), which is less than 1 km from the bison unit. These include all possible periods from day 100 to 275 (30 March to 2 October) with a minimum period length of 15 d with 5-d increments for start and end dates. A forward stepwise regression model was run to explain response variables and precipitation during all 820 periods. The critical climate period that explained the highest sums of squares was selected first and then the period with the second highest sums of squares selected next if it was significant at $p < 0.05$ and did not overlap with the previously selected critical climate period. After the final model was selected, we found no additional effect on weight gain of mean temperatures using the same critical climate period approach. All statistics were computed in JMP 8.0.2 (SAS Inst.).

Results

Bison weight gain

From 2000–2010, 225 different adult female bison of known age and reproductive status were weighed in the fall an average of 4.8 times with 14% having been weighed at least nine times. At the fall weighing, the average age (7.7 years) adult female weighed 437.9 kg and had gained 11.9 kg since the previous year. Weight gain declined as animals aged ($-1.8 \text{ kg year}^{-1}$) and was lower for heavier animals (-0.16 kg kg^{-1}). Weight gain was also dependent on whether adult females had a calf that year or not. The average-aged cow that did not have a calf gained 29.9 kg while those that had a calf gained only 0.6 kg, with this difference narrowing on average by 1.0 kg year^{-1} for every additional year of age. For example, 3.5-year old females that did not have a calf gained 68.1 kg while those that did gained only

15.1 kg. In contrast, 12.5-year old cows gained 7.3 kg if they didn't have a calf and lost 13.5 kg if they did. Standardizing for animal age, previous weight, and whether they had a calf or not, adult female weights varied during 2000–2010 by 43.1 kg (422.9–464.0 kg).

From 2000–2010, 78 adult male bison in total were weighed in the fall with each individual being weighed an average of 3.3 times as an adult. The average 7-year old adult male bison weighed 642.5 kg with a standardized annual weight gain of 65.4 kg. Animals that were heavier the previous year gained less weight in the current year (-0.03 kg kg^{-1}) and weight gain declined with age ($-20.5 \text{ kg year}^{-1}$). Weight gain among years varied nearly two-fold, from 46.5 to 91.3 kg. After being standardized for differences in age and previous weights, adult male weights averaged from 623.6 to 668.4 kg among years. The weights of calves and yearlings could be analyzed over a longer time period, but showed similar amounts of variation in weights and weight gain as adult bison did. From 1994–2010, after standardizing among years for differences in sex ratios, calves varied in weight by 45 kg (113.0–158.2 kg) among years. From 1995–2010, after standardizing among years for differences in sex ratios and previous year's weight, yearlings varied in their weight by 47.5 kg (234.1–281.6 kg).

Weights of the different sex and age classes were synchronous across years as pairwise correlations among all combinations of standardized weights for the four classes (calves, yearlings, adult males, adult females) were significant ($p < 0.05$ for all cases; average $r = 0.75$; Fig. 1). Analysis of the critical climate periods for weight gain of the different age and sex classes reveal consistent positive effects of late-season precipitation paired with consistent negative effects of mid-season precipitation (Fig. 2). After standardizing among years for differences in average ages and reproduction, for adult females, weights were greater in years with more late season precipitation (0.18 kg mm^{-1} ; 29 Jul–23 Aug; Fig. 3), but less in years with more mid-season precipitation (-0.11 kg mm^{-1} ; 19 Jun–14 Jul; Fig. 3). Interannual-variation in precipitation affected the weight gain of adult males in similar manners. For adult males from 2000–2010, more late-season precipitation increased weights (0.20 kg mm^{-1} ; 3 Aug–23 Aug; $p < 0.001$; Fig. 3), but more mid-summer precipitation lowered weights (-0.13 kg mm^{-1} ; 19 Jun–29 Jul; $p = 0.003$; Fig. 3).

Similar to previously described patterns, calf and yearling weights were influenced by precipitation in a similar manner as adult weights. Additional late growing-season precipitation increased the weights of both calves (0.16 kg mm^{-1} ; 8 Aug–28 Aug; Fig. 3) and yearlings (0.16 kg mm^{-1} ; 29 Jul–23 Aug; Fig. 3). In contrast, greater mid-season precipitation for both calves (24 Jun–9 Jul) and yearlings (9 Jun–19 Jul) led to lower weights in the fall (-0.13 and -0.04 kg mm^{-1} , respectively; Fig. 3).

Calving rates

In general, years where bison weighed the most in the fall were followed by high calving rates the next year, with similar effects of the timing of precipitation as observed for bison weights (Fig. 4). Between 1995–2010, 65.5% of adult females had calves in a given year. Calving rates varied

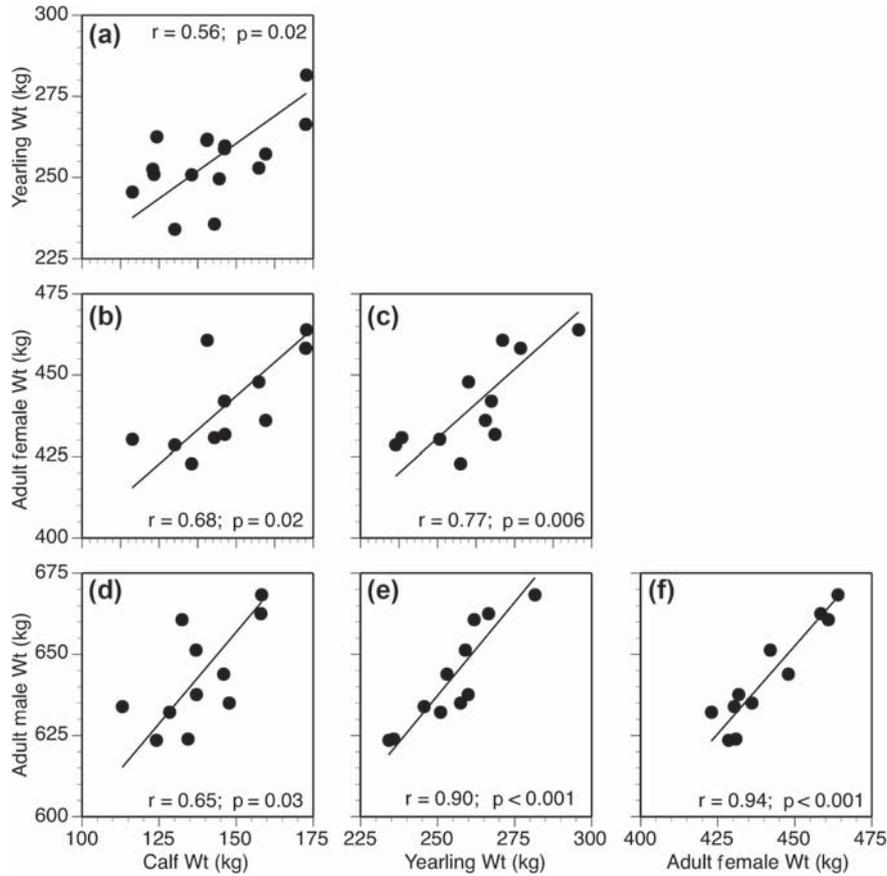


Figure 1. Relationships between interannual variation in weights of different age and sex classes of bison at Konza Prairie.

almost two-fold among years, from 43.8% to 83.1% of the adult female bison reproducing. Calving rates were correlated with the previous year's weights and weight gains for all four classes (Fig. 3). Greater mid-season precipitation (9 Jun–29 Jun) led to lower calving rates the following year ($-0.08\% \text{ mm}^{-1}$), while greater late-season precipitation (3 Aug–23 Aug) led to higher calving rates the following year ($0.11\% \text{ mm}^{-1}$; Fig. 3).

Grass production and flowering

In contrast to bison performance, the critical precipitation periods for aboveground productivity and flowering at Konza were broad and there was never a negative influence of precipitation on either (Fig. 2). ANPP was assessed each year for 25 years (1984–2008) in an annually-burned, ungrazed watershed. For the shallow-soil uplands, ANPP

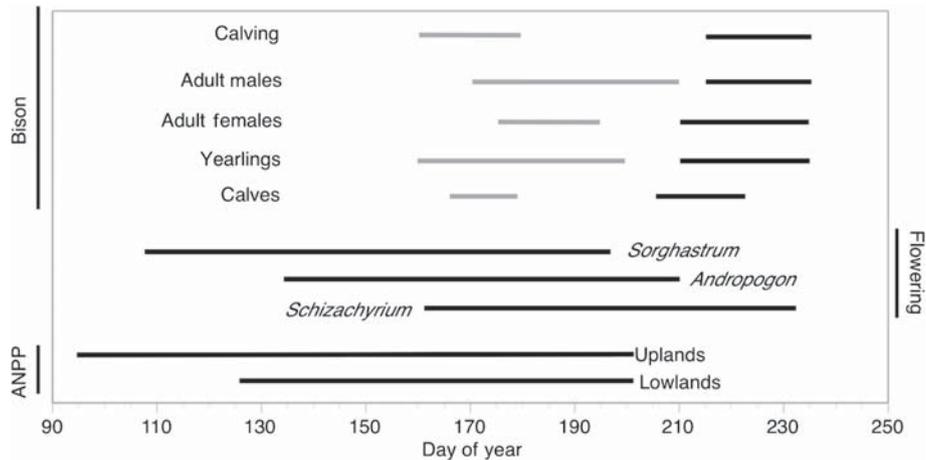


Figure 2. Critical precipitation periods for bison performance, grass flowering, i.e. culm production, and grass aboveground net primary productivity (ANPP). Bison performance includes calving rates of adult females in the following year as well as standardized weights for different age and sex classes in the current year. Gray bars represent negative effects. Black bars represent positive effects.

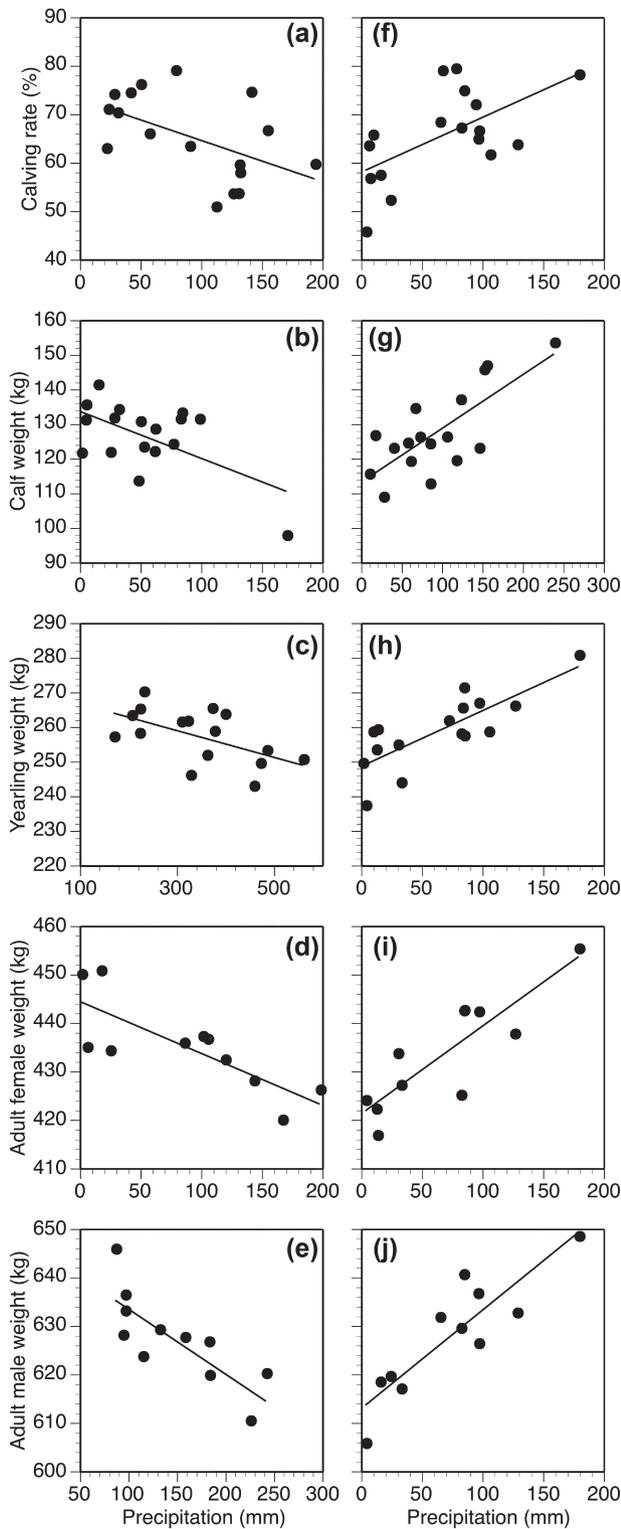


Figure 3. Relationships between bison performance metrics and midsummer precipitation (a)–(e) or late-summer precipitation (f)–(j). Weights and calving are standardized for variation in the other critical climate period. See Fig. 1 for critical climate periods used for each metric.

increased with precipitation from 5 April to 3 August (Table 1). In the deeper-soil lowlands, ANPP increased with precipitation from 10 May to 3 August (Table 1). Flowering of three dominant C_4 grasses was assessed over 27 years (1984–2010)

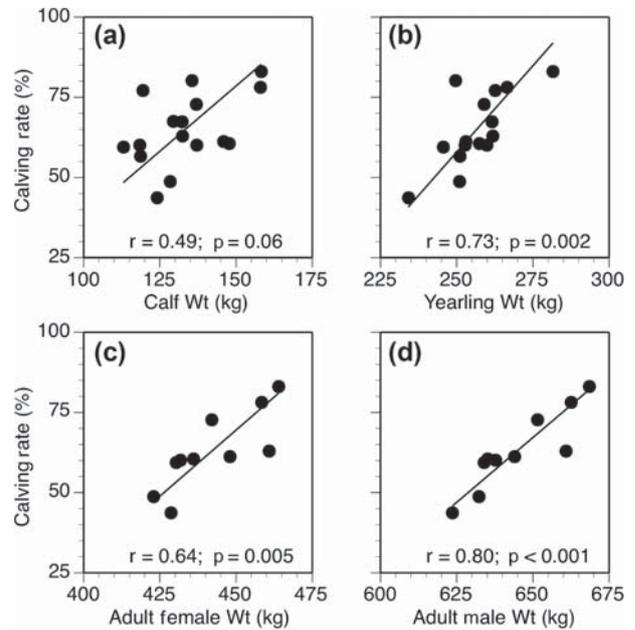


Figure 4. Relationship between weights of bison and calving rates (number of calves weaned relative to the number of adult (≥ 3.5 years) females).

in the same annually-burned, ungrazed watershed as ANPP was measured. As seen before, *Sorghastrum* responds to early precipitation (20 April–29 July), *Schizachyrium* responds to late precipitation (19 June–7 September) and *Andropogon* to precipitation during an intermediate period (20 May–13 August) (Table 1).

Although growing season precipitation was a strong driver of ANPP and flowering of the dominant grasses, bison performance did not respond to interannual differences in total precipitation or within-season precipitation variability

Table 1. Critical precipitation periods (day of year) for grass ANPP for uplands and lowlands, and culm production. Also included are model estimates for critical precipitation periods divided into thirds. Shown are the model coefficients of determination (r^2) and the estimates of the slopes of the relationship between grass ANPP and precipitation ($\text{g m}^{-2} \text{mm}^{-1}$).

Critical precipitation period	Estimate	p
Upland ANPP ($r^2 = 0.70$)		
Day 95–215	0.59 ± 0.08	<0.001
Upland ANPP thirds ($r^2 = 0.71$)		
Day 95–135	0.54 ± 0.19	0.008
Day 135–175	0.61 ± 0.16	0.001
Day 175–215	0.67 ± 0.14	<0.001
Lowland ($r^2 = 0.47$)		
Day 130–215	0.93 ± 0.22	0.002
Lowland thirds ($r^2 = 0.49$)		
Day 130–155	0.99 ± 0.39	0.02
Day 155–185	0.64 ± 0.37	0.09
Day 185–215	1.37 ± 0.39	0.002
<i>Sorghastrum</i> ($r^2 = 0.64$)		
Day 110–210	0.08 ± 0.01	<0.001
<i>Andropogon</i> ($r^2 = 0.39$)		
Day 140–225	0.05 ± 0.01	<0.001
<i>Schizachyrium</i> ($r^2 = 0.44$)		
Day 170–250	0.06 ± 0.01	<0.001

during the growing season. There was no relationship between interannual variation in precipitation during either the upland or lowland ANPP critical climate periods and weight gain of any class of animal ($p > 0.1$ for all comparisons; Fig. 5). Likewise, critical climate periods for flowering explained no significant amount of variation in bison performance ($p > 0.1$ for all comparisons).

Grass quality

In both 2009 and 2010, grass protein concentrations were high enough for adult bison to gain weight for only 100–125 days (Fig. 6). Although 2010 precipitation during the mid-season critical climate period for adult female weights was greater and adult cows gained less weight in 2010 than in 2009, integrated crude protein availability ranged from 10% higher (4 May–1 Aug) to 24% higher (20 April–1 Aug) in 2010 vs 2009.

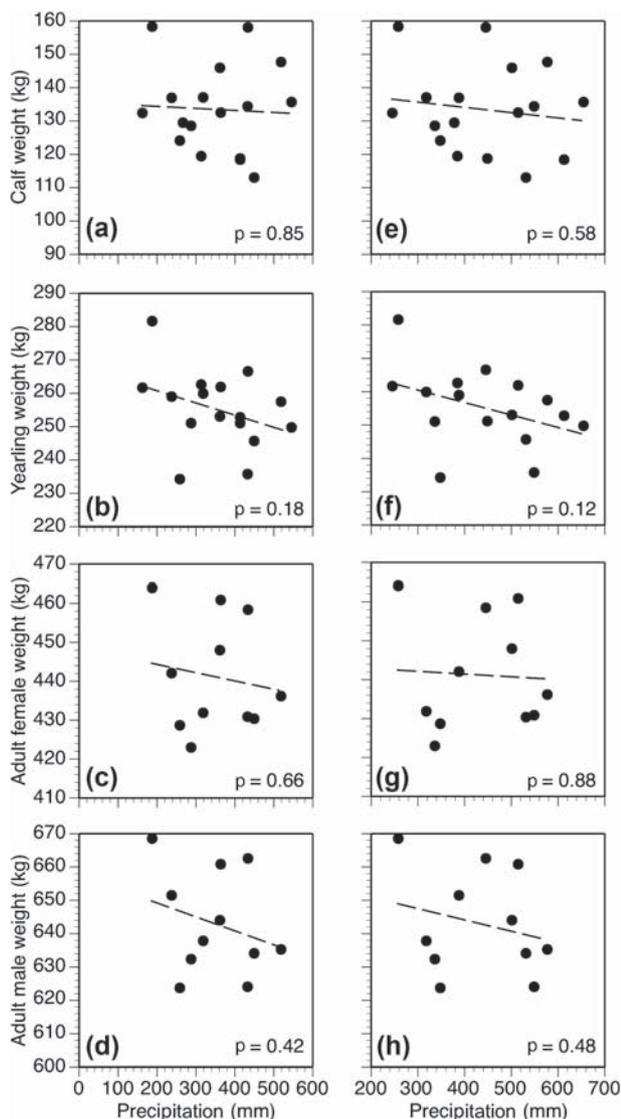


Figure 5. Relationship between bison weights and growing-season precipitation derived from critical precipitation periods of grass ANPP in (a)–(d) upland and (e)–(h) lowland topographic positions.

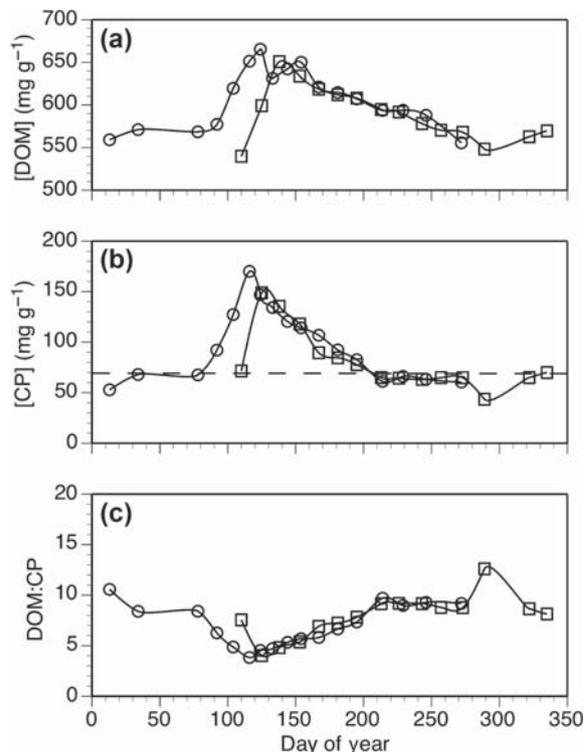


Figure 6. Seasonal patterns of digestible organic matter (DOM) (a), crude protein (CP) (b) and the ratio of DOM:CP for adult female bison (c). Open squares are from 2009 and open circles from 2010. A DOM:CP ratio of 4 is considered optimal for bison growth with higher ratios reflecting increasing protein limitation. The dashed lines represent (a) the approximate minimum CP concentration required for bison to maintain weight, and (c) DOM:CP of 4.

Discussion

For bison at Konza, shifts in the timing of precipitation during the growing season have little effect on primary productivity or grass flowering, but can greatly impact the weight gain of young and adult bison as well as the reproduction of adult female bison. As shown for young bison (Craine et al. 2009), shifting precipitation from late in the growing season to midseason (even with no changes in amounts of precipitation) reduces the weight gain and reproduction of bison. The lack of coherence in critical climate periods for production of grass biomass and bison performance suggests climate variability impacts performance via grass quality not quantity. Differences in dietary quality assessed biweekly between two years were unable to explain variation in weight gain for those two years.

Previous research into the timing of precipitation has focused primarily on the role of precipitation in determining the length of the growing season in ecosystems with a dry season (Chou et al. 2008) or on the balance between winter and summer precipitation (Reynolds et al. 1999, Robertson et al. 2009). This research is the first to show the generality of the importance and uniqueness of shifts in timing within a growing season for grazer performance. As such, future projections of grassland dynamics and the provision of ecosystem services will require not only

predictions of total precipitation and precipitation variability, but also the timing of precipitation within the growing season. The best predictions of how grazer productivity will change under global change scenarios have been ambiguous (Easterling et al. 2007) with little recognition of the importance how changes in precipitation might affect grazer productivity beyond the potential for increased droughts. Current knowledge of spatial patterns of herbivore biomass generate predictions that the biomass of large mammalian herbivores would increase with precipitation, regardless of when it fell during the growing season (McNaughton et al. 1989, Fritz and Duncan 1994). For understanding grazer performance at least in the humid prairies of North America, forecasts of changes in total precipitation or precipitation variability are likely to provide little predictive power.

The geographic extent of the specific predictions of the importance of timing of climate variability remains to be seen. Currently, conservation herds of North American bison are distributed widely, covering a bioclimatic range of more than 20°C mean annual temperature and 750 mm of mean annual precipitation. Although similar patterns of climate sensitivity were observed for the performance of juvenile bison at Tallgrass Prairie Preserve in Oklahoma, which has approximately 2500 bison and is 300 km south of Konza, climate sensitivity is likely to be markedly different for bison present at opposite ends of the climate spectrum. More direct long-term measurements of performance will be required for other bison herds to understand the geographic patterns of climate sensitivity of bison performance.

Our research focused on bison, but the fundamental principles should also apply to cattle and other ungulates (Towne et al. 2005, Hamel et al. 2010). It has long been known that seasonal climate patterns and their effects on seasonal quantity and quality of grass are important for determining how to manage cattle in North America (Vavra and Raleigh 1976), and this work extends this approach to understanding interannual rather than spatial variation in climate. While grazers in unmanaged xeric grasslands are more likely to be limited by the quantity of grass available than its quality (Breman and de Wit 1983), across North America, average grass protein concentrations are greater for cattle in humid regions than xeric ones, which will make further testing on the roles of precipitation timing and grass quality necessary (Craine et al. 2010b).

Analyses of grass quality through fecal spectral composition reinforced previous analyses of the rapid decline of forage quality for regional tallgrass prairie (Rao et al. 1973). At Konza, forage quality drops quickly to maintenance if not sub-maintenance levels, with nitrogen stress being greater for nutrient-demanding individuals such as lactating mothers. The negative effects of greater mid-summer precipitation and even the positive effects of late-summer precipitation on bison performance most likely manifest through changes in forage quality. Although other factors such as forage water content can affect grazer weight gains, a small decline in CP would be enough to explain observed variation in weight gain among years. For example, using a model of nutrient balance and weight gain parameterized for bison, a decline in CP from 70 to 60 mg g⁻¹ (1.12% N to 0.96% N) over 30 d is enough to reduce an adult female

bison weight gain by 17 kg. As such, rather than greater mid-season precipitation immediately lowering grass quality, it might cause bison to lose weight faster at the end of growing season rather than gain weight more slowly earlier, for example, by increasing the production of low-protein culms (Craine et al. 2010a).

Despite the likely role of dietary quality in driving inter-annual variation in performance, comparing dietary quality curves between 2009 and 2010 did not explain the greater weight gain that was observed in 2009. It is uncertain whether bison were unable to successfully incorporate the high-protein grass in 2010 or whether bison later in the growing season had to expend greater energy in 2009 to acquire forage of similar quality as 2010. Likely, more continuous monitoring of weight gain will be necessary to understand when differences in weight gain within the year arise among years. Also, the calibrations between forage quality and fecal spectroscopic characteristics that were used here were derived from cattle. Although bison and cattle are similar to one another, future work could generate bison-specific calibrations to determine whether the mismatch in observed dietary quality and bison performance observed for the two years could be resolved with more finely-tuned calibrations.

In all, accurate forecasts of grassland dynamics will likely have to progress beyond predicting total precipitation or precipitation variability in order to predict future grazer performance. The potential lag between precipitation and nutritional stress offers the potential for integration of current weather, no less near-term forecasts into management decisions. As drought during the middle of the growing season can increase grazer performance, if better predictions of how within-season precipitation might vary can be generated, policy-makers and ecosystem managers might have the potential to mitigate or adapt to future changes in precipitation distribution better. At the center of any future model development will need to be an explicit incorporation of grass quality. As grass protein concentrations may already be experiencing long-term declines (McLauchlan et al. 2010), understanding how they might change in the future will require a better understanding of nitrogen cycling and plant ecophysiology if models are to generate mechanistic responses to multiple forcing factors such as elevated atmospheric CO₂, nitrogen deposition, and warming that are likely to interact with changes in precipitation amounts, variability and timing.

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