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Consequences of climate variability for the performance of bison in tallgrass prairie

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Abstract

Climate variability is a major structuring factor in grassland ecosystems, yet there is great uncertainty in how changes in precipitation affect grazing herbivores. We determined how interannual variation in the timing and magnitude of precipitation affected the weight gain of free-roaming bison in their first and second year. Bison weights were analyzed for 14 years for Konza Prairie, Kansas, and 12 years for Tallgrass Prairie Preserve, Oklahoma. Greater late-summer precipitation increased bison weight gain. For every 100 mm precipitation, weight gain increased 6.4–15.3 kg depending on age classes and site. In contrast, greater midsummer precipitation decreased weight gain. For every additional 100 mm precipitation, weight decreased 9.7–17.3 kg depending on age class and site. The decreased weight gain of bison with greater midsummer precipitation was associated with increased grass stem production during the period for each of three dominant grasses at Konza Prairie. Although greater stem production increases the quantity of aboveground biomass, it should decrease the overall nutritional quality of biomass to grazers, which would reduce weight gain. With offsetting effects of mid- and late-summer precipitation on weight gain, these results show that predicting the effects of climate change on grazers must incorporate both the timing and magnitude of changes in precipitation and their effects on both the quantity and quality of biomass.

Keywords: bison, climate change, grazing, Konza Prairie, Tallgrass Prairie

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Introduction

Globally, variability in precipitation is a major structuring factor for grassland ecosystems (Knapp & Smith, 2001; Weltzin *et al*., 2003; Nippert *et al*., 2006; MacDougall *et al*., 2008). Models of future climate in grasslands vary in their predictions of growing season precipitation (Easterling *et al*., 2000; Smith *et al*., 2005), yet we have a poor understanding of the consequences of potential changes in the magnitude and timing of precipitation for not only plants but also grazers (Soussana & Luscher, 2007; Tietjen & Jeltsch, 2007). Grazers such as North American bison are of conservation and economic importance, and are keystone components that regulate many important aspects of grasslands (Knapp *et al*., 1999; Freese *et al*., 2007). Consequently, any predictions of the functioning of grasslands under future climates must explicitly incorporate how changes in climate affect grazers.

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The effects of precipitation on grazers will depend on changes in the quantity and quality of available plant biomass. In general, ungulate biomass is greater in sites with greater precipitation (Fritz & Duncan, 1994), suggesting that if changes in the timing or magnitude of precipitation increase aboveground production, herbivore performance should also increase. Yet, herbivore growth is often limited by plant nutritional quality – the concentrations of available energy and protein in plant tissues (Van Soest, 1994; Cote & Festa-Bianchet, 2001). If changes in the magnitude and timing of precipitation alter plant quality, these effects could override the consequences of climatic variability on the quantity of food available to grazers. For example, although reduced precipitation can increase foliar N concentrations (Mattson & Haack, 1987; Milchunas *et al*., 1995; Joern & Mole, 2005), reduced precipitation also has the potential to decrease foliar N concentrations through lower soil N mineralization, lower plant uptake, and premature resorption of N (Heckathorn & Delucia, 1996; Turner *et al*., 1997).

In order to understand the role of interannual variation in precipitation on the weight gain of ungulates, we examined long-term records of bison weights from two herds in the tallgrass region of North America: Konza Prairie located in the Flint Hills ecoregion of Kansas and Tallgrass Prairie Preserve located approximately 300 km south of Konza in the Osage Hills ecoregion of Oklahoma. The 14- and 12-year records of weights from Konza and Tallgrass, respectively, comprise the longest continuous records of nondomesticated grazing herbivores known.

For each preserve, we examined variation among years in calf weights after their first summer and the weight gain of calves through their second summer, i.e. yearling weight gain. Beyond its economic importance, weight is positively associated with dominance in adults (Roden *et al*., 2005) and reproductive success in females (Lott & Galland, 1987; Vervaecke *et al*., 2005), whereas weight can be negatively associated with mortality in juvenile grazers (Andersen & Linnell, 1998; Cote & Festa-Bianchet, 2001). We restrict our analyses here to the weights of bison calves and yearlings, which should be most closely tied to variation in environmental factors, as they are the least impacted by resource allocation to reproduction. To test the importance of variation in precipitation to weight gain at different times of the year, we determined the impact of precipitation differences in early-, mid-, and late growing season. The effect of the timing and magnitude of precipitation and burning to predict calf weights and yearling weight gain were evaluated. Burn regimes differ between the two reserves, allowing us to test the importance of climate variability for herbivore performance for two major regional management regimes. To begin to understand some of the proximal controls over weight gain, we also analyzed the relationships between climate and grass flowering from a long-term record at Konza. Grass stems have lower nitrogen concentrations than leaves (Illius & Gordon, 1991; Jung & Vogel, 1992; Craine *et al*., 2002), and could be a link between interannual variation in climate and bison weight gain.

Methods

Study sites

Bison weight gain patterns were assessed for Konza Prairie and Tallgrass Prairie Preserve. Konza Prairie (39°05′N and 96°35′W) is a 3487 ha preserve located in the northern Flint Hills ecoregion in Kansas. 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 4 years. The dominant grasses at Konza include *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*. Bison are collected into a single corral each November, each individual weighed on an electronic chute scale, and calves are fitted with a uniquely numbered ear tag. Animals feed on natural vegetation available to them at the site and are not supplemented except when held in corrals for short periods before weighing. Since 2000, female calves have received calfhood vaccinations and all animals have received injections to control parasites. At this time, most 2-year animals are removed from the herd as well as males older than 7 years and females that are either 15 years old and have not calved in the previous 2 years. The sex ratio of mature females to males is maintained at approximately 5 : 1. After an average of 3 days in the corrals, animals are released back into the bison unit.

The Tallgrass Prairie Preserve (36°50′N and 96°25′W) is a 15 837 ha preserve located in the southern Flint Hills ecoregion (locally known as the Osage Hills) in Oklahoma. In 1993, 300 bison were introduced to a 1977 ha portion of Tallgrass. Since then, additional introductions and natural population growth has led to a population size of 2500 animals by November 2007. To keep the area per animal relatively constant, the area the bison had access to has increased in conjunction with herd growth. Since 2004, bison have been enclosed within 8544 ha. In contrast to the burning regime at Konza, different areas are burned at similar frequencies at Tallgrass, yet the timing of the burn for a given area varies among years. From 1993 to 2007, on average 12% has burned in the spring, 6% in the summer, and 8% in the fall. Other conditions and handling of animals at Tallgrass are similar to Konza. Dominant grasses include *A. gerardii*, *S. nutans*, and *S. scoparium*. Animals are not supplemented nutritionally. Bison are collected into a central corral in early November, sorted, and each individual tagged in their ear. Tallgrass bison are also vaccinated for several bovine viral diseases, treated for internal parasites, and provided hay while in their multiple-day stay in the corral. Like Konza, animals are removed from the herd based on age: males at 6.5 years and females at 10.5 years. All calves and yearlings are retained, replacement heifers and bulls selected at 2.5 years of age with the remaining animals culled from the herd. Weight data for 2004 are excluded due to mismatches in the timing of burning and bison access to newly burned areas – animals were not given access to most newly burned area until midsummer, apparently overriding climate controls over weight gain that year. Although calf weights were predicted well with climate periods in 2004, yearling weight gain that year was 19 kg lighter than expected.

Statistical analyses

Critical precipitation periods for weight gain 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. In analyzing weight data at a site, both calf weight and yearling weight gain were averaged each year by sex. Precipitation data at Konza were taken from a weather station located adjacent to headquarters (ATP01), whereas Tallgrass data were acquired from the Oklahoma Mesonet Foraker station adjacent to preserve headquarters. At each site and each year, total precipitation was determined for 820 periods. These include all possible periods from day 130 to 276 (30 May–3 October) with a minimum period length of 7 days with 3-day increments for start and end dates, e.g. 30 May–6 June, 30 May–9 June, etc. A stepwise regression model was run to explain the mean weight or weight gain for males and females by sex, area burned in each category, and precipitation during all 820 periods. Only significant predictors were retained in the final model. Additional models that included early-season precipitation (before 30 May) showed no effect of variation in precipitation during these periods on weights. After the final model was selected, we found no additional effect on weight gain of mean temperatures during the same 820 mid-and late-season climate periods or mean temperature for different periods earlier in the season. Beyond climate, we found no effect of population density on weight gain, both with number of animals per unit area and animal unit month estimates (data not shown). All the statistics were computed in JMP 7.0.1 (SAS Institute, Cary, NC, USA).

Flowering data

At Konza, in addition to bison weights, flowering of the three most abundant grasses (*Andropogon*, *Schizachyrium*, and *Sorghastrum*) was measured from 1994 to 2006. Stem biomass of the three grass species is measured annually in October in 432 0.25 m^2 quadrats distributed across 72 transects in 18 ungrazed watersheds that are burned at different times of year and frequencies. For each quadrat, the number of stems is counted of each of the three grass species, stems are clipped to ground level, and later dried and weighed. Flowering stem biomass was averaged across all watersheds and transects for each year before analyses. Flowering was largely coincident among watersheds with different fire frequencies among years. For example, in a principal components analysis of flowering among watersheds, a single axis explained 73% of the variation over time in stem biomass with all watersheds having the same sign in the first eigenvector.

Results

At Konza, lower midsummer precipitation led to greater weight gain in both calves and yearlings (Fig. 1). Of the 914 calves weighed from 1994 to 2007, their weight averaged 131 kg in a given year and varied by 45 kg among years (Table 1). During the 15-day critical midsummer climate period (27 June–11 July), precipitation ranged from 1 to 187 mm. Across years, every 100 mm increase in midsummer precipitation decreased body mass by 17.3 kg. For the 713 yearlings also weighed as calves, yearling weight gain averaged 119 kg and varied by 47 kg among years. Yearlings were also susceptible to high midsummer precipitation as weight gain decreased at a rate of 10.5 kg per 100 mm of precipitation. The previous year's weight of a calf had minimal impact on its weight gain as a yearling, independent of gender ($P > 0.1$).

Similar to Konza, lower midsummer precipitation increased the weight gain of both calves and yearlings at Tallgrass. Of the 4538 Tallgrass calves weighed between 1996 and 2007, the average calf weight in a given year was 151 kg and varied by 27 kg among years (Table 1). Precipitation during the 21-day critical midsummer climate period (21 June–11 July, Table 2) ranged from 7 to 227 mm. Every 100 mm increase in midsummer precipitation decreased calf weight by 9.7 kg. Of the 3512 Tallgrass yearlings that were also weighed as calves, high midsummer precipitation decreased weight gain of 13.6 kg per 100 mm. Similar to Konza, calf weight explained little of the variation in yearling weight gain in a given year, although for every 10 kg less a calf weighed, they gained an additional 0.9 kg the following year ($r^2 = 0.004$, $P < 0.001$).

In contrast to midsummer precipitation, high late-summer precipitation increased bison weights. For Konza calves, precipitation during the late-summer critical climate period (11 August–28 August) varied by over 175 mm and each 100 mm increase in precipitation during this period was associated with a 15.3 kg increase in calf weights. For Konza yearlings, weight gain was also positively associated with late-summer precipitation, increasing at a rate of 14.1 kg per 100 mm of addition precipitation. At Tallgrass, late-summer precipitation (11 August–21 September) increased calf weights (6.4 kg per 100 mm) and yearling weights (7.8 kg per 100 mm). At neither site was there an effect of variation in early-season precipitation or air temperatures on weights (data not shown) nor did variation in midsummer precipitation affect the influence of late-summer precipitation on bison weight gain. We found no effect of winter temperature or precipitation on calf weights or yearling weight gain (data not shown).

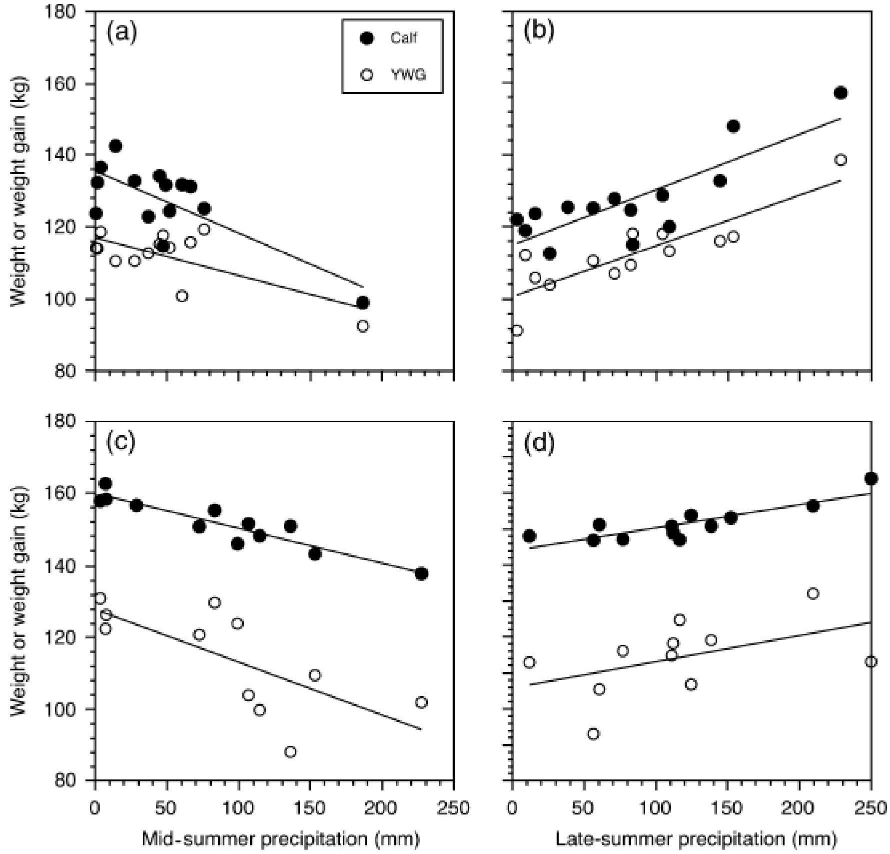

Fig. 1 Relationships between mid- (a, c) and late-summer (b, d) precipitation and bison weights for each year for Konza Prairie (a, b) and Tallgrass Prairie Preserve (c, d). Calf weights and yearling weight gain (YWG) were adjusted for differences in sex ratios to represent the average weight of an average male and average female bison. Midsummer weights were standardized for variation in late-summer precipitation and vice versa. See Table 2 for regression equations.

A long-term dataset from Konza on flowering stem production in the dominant three grasses suggests that greater stem production associated with more flowering in years with high midsummer precipitation could contribute to lower weight gain by decreasing plant protein concentrations. From 1994 to 2006, greater precipitation in midsummer was associated with greater stem mass per unit ground area for each species (Fig. 2). The midsummer critical precipitation period for stem biomass was calculated to be 14 June–8 July compared with 21 June–11 July for bison weight gain at Konza. Stem biomass density for *Andropogon*, *Schizachyrium*, and *Sorghastrum* increased at a rate of 12.2, 3.9, and 10.2 $g\,m^{-2}$ per 100 mm of midsummer precipitation, respectively ($r^2 = 0.79$, 0.74, 0.73; $P < 0.001$ for all).

Although there was more variation in burning among years at Tallgrass than Konza, the amount of area burned in a given season or among seasons explained no additional variation in calf weight or yearling weight gain ($P > 0.05$ for all). In addition, although bison in most years had access to areas burned in the summer and autumn, Tallgrass bison were also susceptible to high midsummer precipitation (Table 2).

Discussion

Although it has been recognized that climate change has the potential to affect the performance of grazers (Easterling *et al.*, 2007), predicting the effects of climate change on grazers has largely been restricted to extrapolating results from grassland experiments conducted in the absence of grazers (Shaw *et al.*, 2002; Fay *et al.*, 2003; An *et al.*, 2005). Because experiments that manipulate climate factors are rarely of the scale to incorporate large grazers or incorporate grazer-induced feedbacks to ecosystem processes, conclusions from these experiments have to be considered in conjunction with spatial or temporal relationships between climate and grazer performance. In analyzing the responses of bison to interannual variation in climate, bison weight gain was dependent on the timing of variation in precipitation with declines in precipitation increasing

Table 1 Annual average calf and yearling weight gain

	Konza				Tallgrass			
Year	*n*	Calf weight (kg)	*N*	YWG (kg)	*N*	Calf weight (kg)	*n*	YWG (kg)
1994	34	$129.4 \pm 25.2^{BCDE*}$						
1995	32	135.9 ± 29.4^{BCD}	18	116.2 ± 16.6^{BCD}				
1996	38	121.0 ± 26.4^{CDE}	29	124.9 ± 20.6^{B}	159	157.0 ± 25.3^{ABCD}		
1997	45	129.0 ± 29.1^{BCDE}	18	129.3 ± 23.2^{ABC}	187	144.1 ± 24.7^{EF}	95	132.6 ± 16.7^{BC}
1998	59	118.6 ± 23.7^{DE}	35	111.5 ± 20.4^{BC}	186	149.9 ± 23.2^{CDE}	119	109.2 ± 21.9^{FG}
1999	55	119.7 ± 27.2^{DE}	51	115.5 ± 20.0^{BC}	176	140.8 ± 28.3^{EFG}	160	115.9 ± 27.6^{EF}
2000	62	128.5 ± 25.9^{BCDE}	53	114.8 ± 27.2^{BC}	296	144.9 ± 30.4^{EF}	163	118.5 ± 29.1^{DEF}
2001	57	132.8 ± 30.7^{BCD}	57	125.3 ± 27.2^{B}	370	158.3 ± 24.2^{ABC}	217	121.4 ± 31.7^{DE}
2002	82	137.1 ± 30.7^{BC}	50	122.0 ± 25.2^{BC}	435	163.0 ± 28.6^{A}	361	150.1 ± 30.0^{A}
2003	98	124.1 ± 27.8^{CDE}	77	96.4 ± 23.2^{D}	596	158.3 ± 26.5^{AB}	419	117.1 ± 26.6^{EF}
2004	57	112.9 ± 26.4^{E}	90	108.0 ± 26.7^{CB}	556	143.1 ± 22.8^{F}	561	99.5 ± 25.2^{H}
2005	77	158.4 ± 24.2^{A}	51	127.4 ± 25.0^{B}	431	149.8 ± 20.8^{DE}	492	127.4 ± 29.0^{CD}
2006	111	159.1 ± 28.7^{A}	76	144.2 ± 26.4^{A}	529	154.4 ± 24.2^{BCD}	418	134.4 ± 29.6^{B}
2007	107	136.3 ± 27.5^{B}	108	122.7 ± 23.5^{B}	617	136.3 ± 23.9^{G}	507	110.5 ± 27.6^{G}
Mean	65	131.5 ± 14.8	55	118.9 ± 13.7	378	150.7 ± 9.0	319	123.0 ± 16.0

*Calf and yearling weight gain (YWG) (± SD) averaged across all animals. YWG is the amount of weight gained by a calf by the end of the second growing season.
Superscript letters denote significant difference among years at $P < 0.05$ via Tukey's HSD test and were performed after standardizing for differences in sex ratios among years.

Table 2 Results of regression for calf weight and yearling weight gain (kg) for Konza Prairie (1994–2007) and Tallgrass Prairie Preserve (1996–2007)

		Calf weight			YWG		
	Range	Estimate	SS	*P*	Estimate	SS	*P*
Konza							
Intercept		127.50		<0.001	112.04		<0.001
Sex (M–F)		11.34	901	<0.001	14.17	1306	<0.001
$Precip_{mid}$	178–192	−0.173	1666	<0.001	−0.105	609	0.002
$Precip_{late}$	223–240	0.154	2462	<0.001	0.141	1993	<0.001
Tallgrass							
Intercept		151.57		<0.001	126.6		<0.001
Sex (M–F)		8.68	452	<0.001	17.60	1619	<0.001
$Precip_{mid}$	172–192	−0.097	953	<0.001	−0.136	1726	<0.001
$Precip_{late}$	223–264	0.064	384	0.002	0.078	550	0.03

Units for $Precip_{mid}$ and $Precip_{late}$ estimates: $kg\,mm^{-1}$.
Coefficients of determination at Konza for calves and yearling weight gain (YWG) were 0.74 and 0.77, respectively; 0.90, 0.68 at Tallgrass.
Estimates are differences between males and females in weights and slopes for relationship between precipitation and weight.
Sums of squares (SS) indicate the amount of variation attributed to each variable.

weight gain if occurring midsummer. The increases in weight gain with reduced precipitation are unlikely to come as a result of decreases in aboveground production, which normally occur with declines in precipitation (Knapp & Smith, 2001). Instead, declines in bison weight gain in years with high midsummer precipitation are more likely explained by lower nutritional quality of grass biomass than lower quantity.

Proximally, one reason nutritional quality might decline in years with greater midsummer precipitation is an increase in flowering stem production. Stems have lower protein and digestible organic matter concentrations than leaves, and a relative increase in stem production lowers the nutritional quality of the grass (Illius & Gordon, 1991; Jung & Vogel, 1992). Just as midsummer precipitation drives greater flowering stem biomass accumulation, replacing midsummer precipitation with stem biomass in regression models yielded little reduction in the total variation in calf weight and yearling weight gain (data not shown). The long-term monitor-

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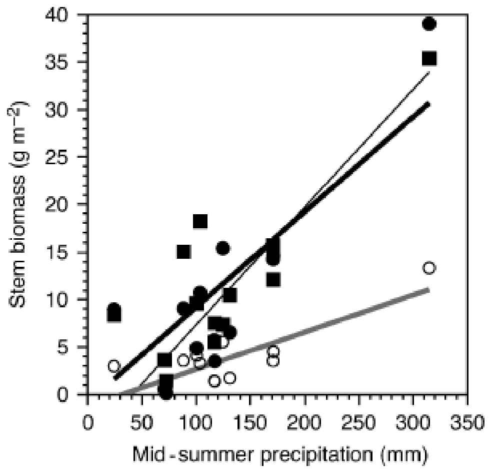

Fig. 2 Flowering and midsummer (14 June–8 July) precipitation *Andropogon gerardii* (closed circle, thick black line; $-0.80+0.123\times$), *Schizachyrium scoparium* (open circle, thick gray line; $0.01+0.039$), *Sorghastrum nutans* (closed square, thin gray line; $2.4+0.102\times$) from 1994 to 2006.

ing of flowering at Konza occurs outside of the area currently occupied by bison. As such, multiple layers of research are required to better understand the negative effects of increased midsummer precipitation on bison performance. Not only does flowering need to be better monitored within the bison unit, but it will also be important to investigate whether the increased stem biomass is a proximal cause of the reduced weight gain in bison as opposed to changes in the nutritional quality of leaves and stems (Jung & Vogel, 1992), or the relative production of grasses and forbs (Briggs & Knapp, 1995). It should also be tested whether greater stem biomass reduced weight gain as a consequence of lower nutritional quality, or changes in forage handling and intake (Drescher *et al*., 2006).

In contrast to the declines in weight gain with greater midsummer precipitation, greater late-summer precipitation increased weight gain. In this instance, greater later-summer precipitation might be increasing weight gain by increasing forage quality as stocking densities at Konza are low to moderate. Even in a year with low late-summer precipitation, grass biomass is still present. A host of potential mechanisms operating at multiple levels are possible here, including delays in senescence, increases in the productivity of C_3 grasses, or increases in N mineralization, which would increase the N concentrations of grasses. In general, a program of remote sensing, detailed field observations, and fecal analyses will be needed to begin to evaluate competing hypotheses for the differential effects of mid- and late-summer precipitation.

The responses of grazers to climate variability are also likely modulated by fire. Burning grasslands can benefit grazers, which preferentially select recently burned areas (Shaw & Carter, 1990; Coppedge & Shaw, 1998; Knapp *et al*., 1999). Yet, in some ecosystems, fire can restrict the quantity and quality of available grass, while reducing the positive effects of grazers on forage quality in adjacent unburned areas (Archibald *et al*., 2005; Anderson *et al*., 2007). We found no evidence that variation in total area burned at either site influenced weight gain or the effect of climate on weight gain. At Konza, watersheds are burned at different frequencies, but there is little variation among most years in the area of watersheds with different fire frequencies burned. Yet, the area of watersheds burned with a 4-year fire return interval varied from 0% to 13% without any significant influence on final weight gain. In contrast to Konza, burning at Tallgrass follows the patch-burn mosaic approach (Fuhlendorf & Engle, 2001), where the long-term frequency of burning is similar among different areas, but the timing of the burning varies with fires set in spring, summer, and autumn.

Even though there was no relationship among years between area burned and weight gain for either site, differences in fire regimes between the sites could contribute to intersite differences in weight gain patterns. Tallgrass calves on average were 15% heavier than Konza calves and were 44% less susceptible to increases in midsummer precipitation. Tallgrass yearlings on average gained 7% less mass than Konza yearlings, while being 30% more susceptible to increases in midsummer precipitation. Whether the differences between sites in weight gain patterns can be explained by differences in burn regimes, site conditions, or herd genetics is unknown, but the lack of influence of interannual variation in fire within sites raises questions about mechanisms underlying the often stated direct advantage of burning to grazers. For example, although bison are attracted to recently burned areas, fires can cause grazers to abandon grazing lawns in areas adjacent to burns (Archibald *et al*., 2005). Abandoning lawns early in the growing season and allowing them to decline in nutritional quality could reduce the availability of high quality forage late in the season and reduce grazer weight gain.

Our results indicate that changes in the timing of precipitation are an important driver in grasslands, for both plants and herbivores. With both regions primarily native grassland supporting over a million cattle, subtle shifts in the timing of precipitation can have large economic effects no less ecological ones. Even with differences in climate, burn regimes, and underlying geology between Konza and Tallgrass, the effects of precipitation on bison weight gain were consistent across sites: increased precipitation in late summer increases bison weight gain, but increased precipitation midsummer decreases bison weight gain. Because of possible offsetting effects of precipitation early and late in the summer on weight gain, general increases or decreases in precipitation could have less effect on the performance of grazers than shifts in the timing of precipitation.

Understanding how changes in the timing of precipitation will affect grazers relies not only on understanding the quantity of food available to them, but also the quality of available forage. In ecosystems where grazers are primarily limited by the quantity of food, reductions of precipitation are likely to decrease herbivore performance (Blanchard *et al*., 2003; Derner & Hart, 2007). When grazers become more limited by biomass quality, reductions in precipitation that increase overall diet quality can increase grazer performance even when total forage biomass decreases (Breman & de Wit, 1983; Sheaffer *et al*., 1992; Ellery *et al*., 1995; Sanderson *et al*., 1997). Predicting when reductions in precipitation will positively affect herbivores will require not only understanding what limits herbivore performance, but also such factors as the phenology of plants and the controls over nutrient supplies and senescence. With the knowledge that reductions in soil moisture in the middle of the growing season reduces stem production, predicted reductions in net water balance, whether through reductions in growing season precipitation or increases in temperature, might actually have a positive effect on grazers in some grasslands. Yet, this will likely depend on the timing of any reductions and how they affect the flowering of grasses. As such, it will be critical for modeling efforts to predict changes not only in the magnitude of precipitation in the future, but also the timing. Advances in modeling seasonal climate will have to be paired with a better understanding of the geographic extent of protein limitation in herbivores in order to predict the effects of climatic variability on herbivore performance.

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