LIVESTOCK AND VEGETATION RESPONSES TO ROTATIONAL GRAZING IN SHORT-GRASS STEPPE

Justin D. Derner^{1,2} and Richard H. Hart¹

ABSTRACT.—There is a paucity of information concerning livestock and vegetation responses to rotational grazing in short-grass steppe. We compared effects between 1995 and 2003 of time-controlled, short-duration rotational grazing against season-long continuous grazing, at a moderate stocking rate (1.95 ha · animal unit month⁻¹), on livestock gains and on foliar and basal cover in short-grass steppe. Livestock average daily gains, grazing-season gains, and beef production did not differ between grazing systems. We observed no relationship between precipitation (annual or growing-season) and average daily gain. In contrast, both grazing-season gains and beef production exhibited a significant curvilinear response to both growing-season and annual precipitation. Basal and foliar cover of all plant functional groups (C₃ annual grasses, C₃ perennial grasses and grass-like, C₄ perennial grasses, cactus, annual forbs, perennial forbs, and shrubs/subshrubs) did not differ between grazing systems. Litter and bare ground were also unaffected by grazing system, with litter increasing and bare ground decreasing over the duration of this experiment. Land managers in short-grass steppe who are implementing rotational grazing at moderate stocking rates should not expect increased livestock gains or changes in basal and foliar cover of the plant community. Rotational grazing may be a useful management tool for achieving conservation goals through modifications of seasonality and intensity of use in paddocks within larger management units to accommodate spatial variability in vegetation and temporal variation in precipitation.

Key words: rotational grazing, season-long continuous grazing, short-grass steppe, short-duration grazing, plant functional groups, basal cover, foliar cover, livestock gain, bare ground.

Traditional rangeland management practices have focused principally on increasing homogeneity of use in pastures through manipulating the distribution of livestock grazing in space and time, and manipulating the stocking rate. Short-duration rotational grazing systems have been implemented on rangelands primarily to achieve greater homogeneity of use (Savory 1988). The intent of these grazing systems is to reduce species-selective grazing (i.e., patch grazing), which occurs at landscape scales as a consequence of continuous grazing under low to moderate stocking rates. Short-duration rotational grazing involves the movement of livestock through a series of small paddocks, thereby imposing short periods of concentrated grazing activity and longer periods of recovery. This grazing system provides greater managerial control over the frequency (number of events) and uniformity (percentage of plants), but not intensity (grazed height), of defoliation through manipulation of the grazing period (Gillen et al. 1990, Heitschmidt et al. 1990a, Derner et al. 1994). From the animal perspective, Hart et al. (1993a) concluded that “rota-

tional grazing systems are unlikely to benefit animal performance unless they reduce pasture size and distance-to-water below previous levels, decrease travel distance and increase uniformity of grazing.”

Short-duration rotational grazing has been the focus of many grazing studies in the Texas Rolling Plains (Wood and Blackburn 1984, Heitschmidt et al. 1987a, 1987b, 1990a, 1990b, Teague and Dowhower 2003), the tall-grass prairie in Oklahoma (Brummer et al. 1988, Gillen et al. 1990, 1998, Derner et al. 1994, Cassels et al. 1995, McCollum et al. 1999), the northern mixed-grass prairie (Hart et al. 1988, 1993a, 1993b, Kirby and Webb 1986, Hepworth et al. 1991, Biondini and Manske 1996, Manley et al. 1997), the fescue grasslands in Canada (Dormaar et al. 1989), and the veld of South Africa (Denny and Barnes 1977, Denny et al. 1977, Gammon and Roberts 1978a, 1978b, 1978c, 1980). How this grazing system affects animal and vegetation responses in short-grass steppe, however, has been little studied (Pitts and Bryant 1987, White et al. 1991). In addition, these previous investigations

¹USDA–Agricultural Research Service, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009.

²E-mail: justin.derner@ars.usda.gov

in short-grass steppe compared short-duration rotational grazing at higher stocking rates to season-long continuous grazing at a moderate stocking rate. Because stocking rate has greater effects on animal and vegetation responses than grazing systems (Van Poolen and Lacey 1979, Derner et al. 1994, Manley et al. 1997, Gillen et al. 1998, McCollum et al. 1999), comparisons between grazing systems with different stocking rates are likely confounded. Due to the paucity of studies investigating grazing systems at similar stocking rates in short-grass steppe, land managers have had to make decisions based on scientific results from more productive rangeland ecosystems or based on inferences drawn from experiences or demonstration projects. Therefore, there is a clear need for an increased understanding of how animals and vegetation respond to short-duration rotational and season-long continuous grazing at similar stocking rates in this rangeland ecosystem.

Amount and seasonal distribution of precipitation markedly influence forage production in rangeland ecosystems, and regression relationships have been developed using precipitation to predict forage production (e.g., Milchunas et al. 1994, O'Connor et al. 2001, Khumalo and Holechek 2005). Forage production feeds back to impact livestock gains through forage availability to grazing animals. Therefore, precipitation is a driver of livestock gains, and its influence is likely magnified during drought conditions when forage availability is low. Largely unclear, however, is how grazing system may mediate the influence of precipitation on livestock gains. Experimental studies conducted over several years having contrasting precipitation can address the effect of grazing system.

Our objective in this 9-year investigation was to compare effects of time-controlled, short-duration rotational grazing against season-long continuous grazing (both at the same moderate stocking rate) on animal gains, foliar cover, and basal cover in short-grass steppe. We evaluated vegetation responses at 2 different topographical positions because lowlands are thought to receive disproportionately greater use relative to uplands, because lowlands exhibit higher productivity combined with a smaller proportion of land area within landscapes. We chose to investigate the effects of grazing system at the moderate stocking

rate because this stocking rate has previously been both profitable and sustainable in short-grass steppe (Hart and Ashby 1998). Based on previous investigations that compared short-duration rotational grazing and season-long continuous grazing at the same stocking rates as in other rangeland ecosystems (e.g., Derner et al. 1994, Gillen et al. 1998, McCollum et al. 1999), we hypothesized that the short-duration rotational grazing system would not significantly influence animal or vegetation responses compared to traditional season-long continuous grazing.

STUDY AREA

The USDA–Agricultural Research Service Central Plains Experimental Range is located about 20 km northeast of Nunn, in north central Colorado (40°49'N, 107°46'W). Mean annual precipitation (1939–2003) is 341 mm and growing season precipitation (May–September) is 243 mm. Total annual precipitation during this study ranged from 243 mm in 2002 to 565 mm in 1997, and growing-season precipitation ranged from 175 mm in 2002 to 442 mm in 1997 (Table 1).

METHODS

The season-long continuously grazed unit consisted of a single pasture of 259 ha. The short-duration rotational grazing unit consisted of 7 paddocks (each 65 ha) combined to total 455 ha. All pastures had been grazed at a moderate stocking rate under season-long continuous (mid-May to mid-October) grazing prior to initiation of this investigation. Hereford and crossbred yearling steers, with initial weights of 259 ± 12 kg $\cdot$ steer⁻¹ across the study years, were stocked at a moderate stocking rate (1.95 ha $\cdot$ animal unit month⁻¹) on both units to remove approximately 40% of the current year's herbage production during the 5-month grazing season each year from 1995 to 2003. This stocking rate resulted in stocking densities of 0.1 animal unit $\cdot$ ha⁻¹. Grazing began in mid-May each year and continued until mid-October, except when drought conditions dictated earlier removal in 2000 (12 September) and 2002 (9 August). Yearling steers were weighed at the beginning and end of each grazing season. The grazing period in each rotational paddock was 6–7 days, resulting in 3 full cycles through the paddocks during each

TABLE 1. Annual and growing-season precipitation, and average daily gain and grazing-season gain for season-long continuous and short-duration rotational grazing systems in short-grass steppe at Central Plains Experimental Range, near Nunn, Colorado (1995–2003). Means are given with 1 standard error (in parentheses); $n = 40$ for continuous grazing, and $n = 70$ for rotational grazing.

Year(s)	Precipitation (mm)		Average daily gain ($\text{kg} \cdot \text{hd}^{-1}\text{day}^{-1}$)		Grazing-season gain ($\text{kg} \cdot \text{hd}^{-1}$)	
	Annual	May–Sep	Continuous	Rotational	Continuous	Rotational
1995	471	399	1.11 (0.01)	1.16 (0.01)	165 (2)	173 (2)
1996	387	294	1.01 (0.02)	1.00 (0.01)	152 (3)	150 (2)
1997	565	442	1.04 (0.02)	1.06 (0.02)	154 (3)	158 (3)
1998	422	277	0.99 (0.02)	0.90 (0.01)	146 (3)	133 (2)
1999	557	375	1.15 (0.02)	1.14 (0.01)	163 (3)	162 (2)
2000	311	228	1.03 (0.02)	0.96 (0.01)	123 (2)	114 (2)
2001	356	258	1.15 (0.02)	1.10 (0.01)	169 (2)	162 (2)
2002	243	175	0.87 (0.02)	0.83 (0.02)	76 (2)	73 (2)
2003	322	218	1.13 (0.02)	1.15 (0.02)	163 (4)	165 (2)
1995–2003	404	296	1.05 (0.03)	1.03 (0.04)	144 (2)	143 (2)
1939–2003	341	243				

grazing season. Grazing began in a different paddock each year.

In 1995 and 2003, measurements of foliar and basal cover were made on four 50-m permanent transects in the pasture of the season-long continuous grazing unit, and on two 50-m permanent transects in each of 2 randomly chosen pastures of the short-duration rotational grazing unit. Half of the transects were randomly located on level upland topographic positions consisting of soils of the Vona series (coarse-loamy, mixed, superactive, mesic Aridic Haplustalfs) with *Bouteloua gracilis* (H.B.K.) Lag ex Steud. as the dominant species. The other half were randomly located on a level-foot slope topographic position consisting of soils of the Avar series (fine-loamy, mixed, mesic Ustic Natrargids) with dominant species including *Sporobolus airoides* (Torr.) Torr and *Distichlis spicata* (L.) Greene. Basal and foliar cover were estimated in mid-August with a 10-point frame, placed perpendicular at each meter along the permanent transect, resulting in 500 measurements per transect for the following functional groups: C_4 perennial grasses, C_3 perennial grasses and grass-like, C_3 annual grasses, perennial forbs, annual forbs, cactus, shrubs (including subshrubs), and litter and bare ground. Species encountered within functional groups are listed in the Appendix. Cover data for each transect were expressed as a percentage of the 500 measurements for each functional group.

There was only a single replication of the season-long continuous grazing pasture. Consequently, inferences about our findings are limited to our experimental location and treat-

ments. The potential statistical consequences and limitations of pseudoreplication have been discussed by Hurlbert 1984 and Heffner et al. 1996. However, the length of this study (9 years) does provide replication in time, and the differences in annual (2.3-fold) and growing-season (2.5-fold) precipitation across the study period provide insights into the role of environmental variation in response to grazing systems. Further experimentation is required to determine the applicability of results to a wider geographic area. Animal gain data were analyzed using analysis of variance (ANOVA) with year, precipitation (annual and growing-season), and grazing system as treatments. Individual animals were considered experimental units. Because basal and foliar cover data were taken on the same transects in 1995 and again in 2003, we analyzed this data using 2-factor repeated measures ANOVA with grazing system and topography as main treatment factors, along with their interaction. We were primarily interested in the significance of the time $\times$ grazing system interaction factor. A significant interaction would indicate that the difference in cover between the 2 sample years could be attributed to the grazing system. Transects were considered experimental units. An α -level of 0.10 was used in all comparisons to determine significance.

RESULTS

Animal Responses

Animal gains, expressed as grazing-season gain ($\text{kg} \cdot \text{hd}^{-1}$) or beef production ($\text{kg} \cdot \text{ha}^{-1}$), differed among the 9 years ($P < 0.0001$), and

between growing seasons ($P < 0.0001$) and annual precipitation ($P < 0.0001$), but did not differ between grazing systems across years (Table 1). Average daily gain ($\text{kg} \cdot \text{hd}^{-1} \cdot \text{day}^{-1}$) differed among the 9 years ($P < 0.0001$), but not for growing-season or annual precipitation, nor grazing system (Table 1). Regression analyses were used to determine the relationship (linear, quadratic, power, or hyperbolic) between precipitation and animal gains. The model with the greatest r^2 value was used as the best fit (Derner et al. 2004). We observed no relationship between precipitation and average daily gain (Fig. 1), likely because animals were removed from study pastures in the drought years of 2000 and 2002 before animal performance was negatively impacted. In contrast, grazing-season gains were influenced by both growing-season and annual precipitation: gains were lower with less precipitation (Fig. 2). Here, the differences in length of grazing season drive this relationship, with shorter grazing seasons due to drought (2000 and 2002) having much lower grazing-season gains. Beef production or gain per unit land area ($\text{kg} \cdot \text{ha}^{-1}$) did exhibit a significant curvilinear response to both growing-season and annual precipitation (Fig. 3). These regression equations indicate that beef production would be optimized when annual precipitation is 491 mm ($24.8 \text{ kg} \cdot \text{ha}^{-1}$) and growing-season precipitation is 368 mm ($25.1 \text{ kg} \cdot \text{ha}^{-1}$). For comparative purposes, the predicted beef production would be $20.3 \text{ kg} \cdot \text{ha}^{-1}$ for the long-term (1939–2003) annual precipitation mean of 341 mm, and $20.0 \text{ kg} \cdot \text{ha}^{-1}$ for the growing-season precipitation mean of 243 mm.

Vegetation Responses

Basal cover of all plant functional groups was similar between grazing systems across topographical positions, which did not differ (Table 2). In addition, bare ground and litter also did not differ between grazing systems. Annual forbs, bare ground, cactus, and litter did exhibit temporal differences: annual forbs (99%), bare ground (61%) and cactus (55%) decreased between 1995 and 2003, while litter increased by 28%. Foliar cover of all plant functional groups also did not differ between grazing systems across upland and lowland topographical positions (Table 2). Foliar cover of annual forbs decreased by 92% from 1995

Fig. 1. Relationships between average daily gain and growing-season precipitation (upper panel) and annual precipitation (lower panel) for season-long continuous and short-duration rotational grazing systems in short-grass steppe at Central Plains Experimental Range, near Nunn, Colorado (1995–2003).

to 2003 and perennial forbs decreased by 70% from 1995 to 2003 (author).

DISCUSSION

Animal Responses

The lack of differences in average daily gain and grazing-season gain of the yearling steers, and in beef production between the season-long continuous and short-duration rotational grazing systems is in agreement with most previous studies. For example, average daily gain of steers in northern mixed-grass prairie was not affected by grazing system (Biondini and Manske 1996); rather, stocking rate was the primary factor influencing gain (Hart et al. 1988, Manley et al. 1997). Similarly, Heitschmidt et al. (1990b) determined that stocking rate, rather than grazing system, was the primary factor affecting livestock production and economic returns on rangelands in the Texas Rolling Plains. Average daily gain of steers on poor-condition short-grass steppe

Fig. 2. Relationships between grazing-season gain and growing-season precipitation (upper panel) and annual precipitation (lower panel) for season-long continuous and short-duration rotational grazing systems in short-grass steppe at Central Plains Experimental Range, near Nunn, Colorado (1995–2003).

Fig. 3. Relationships between beef production and growing-season precipitation (upper panel) and annual precipitation (lower panel) for season-long continuous and short-duration rotational grazing systems in short-grass steppe at Central Plains Experimental Range, near Nunn, Colorado (1995–2003).

decreased by 40% when the short-duration rotational grazing system employed a doubled stocking rate compared to the season-long continuous grazing system (Pitts and Bryant 1987). However, average daily gain did not differ between season-long continuous and short-duration rotational grazing when the rotational grazing system was stocked at 1.5 times that under continuous grazing (Pitts and Bryant 1987). In contrast, short-duration rotational grazing in high-seral-condition tallgrass prairie of Oklahoma reduced gain per steer by 11% under a moderate stocking rate and by 20% under a heavy stocking rate (McCollum et al. 1999). This reduction in individual animal performance with short-duration rotational grazing resulted in lower gains per hectare for rotational compared to season-long continuous grazing for all stocking rates. These authors attributed the reduced performance to decreased forage intake (McCollum et al. 1999). This idea is supported by Kirby and Webb (1986), who determined that diet composition

under short-duration rotational and season-long continuous grazing did not differ. Though we did not directly measure diet composition or forage intake, the lack of difference in animal performance between grazing systems leads us to infer that diet composition and forage intake of yearling steers did not differ. Both growing-season precipitation and annual precipitation influenced grazing-season gains and beef production, but not average daily gain. Gains did not increase linearly with increasing precipitation, however. Rather, the relationship was curvilinear, suggesting that above-average precipitation does not translate into greater animal gains in this rangeland ecosystem. Because livestock were removed early in the grazing season in 2000 and 2002, the negative effects of this limited precipitation on average daily gains were not manifest. The negative effects were, however, evident for grazing-season gain and beef production because of the shortened grazing season.

TABLE 2. Average basal and foliar cover by functional group for season-long continuous and short-duration rotational grazing systems in short-grass steppe at Central Plains Experimental Range, near Nunn, Colorado, in 1995 and 2003. Means are given with 1 standard error (in parentheses); $n = 4$.

Functional group ^a	1995		2003		Time <i>P</i> -value	Time × grazing system <i>P</i> -value
	Continuous	Rotational	Continuous	Rotational		
Basal cover (%)						
AF	2.2 (1.6)	0.8 (0.1)	0.1 (0.1)	0	0.0939	0.3654
Bare ground	22.4 (7.2)	21.6 (3.0)	8.3 (2.1)	9.0 (4.1)	0.0639	0.8934
C ₃ AG	0.2 (0.1)	1.5 (1.2)	0.1 (0.1)	0	0.2361	0.2915
C ₃ PG	1.0 (0.5)	3.1 (1.2)	1.4 (0.2)	2.7 (0.7)	0.9654	0.7079
C ₄ PG	20.2 (3.4)	9.8 (1.4)	16.4 (2.1)	10.4 (1.7)	0.4678	0.3388
Cactus	0.6 (0.4)	1.2 (0.8)	0.2 (0.2)	0.7 (0.6)	0.0470	0.6570
Litter	52.5 (8.4)	60.4 (3.3)	72.0 (4.3)	73.0 (3.0)	0.0245	0.4910
PF	0.9 (0.5)	0.4 (0.2)	0.1 (0.1)	0.1 (0.1)	0.1344	0.4426
Shrub	0.2 (0.2)	0.3 (0.2)	0	0.1 (0.1)	0.1648	0.8203
Foliar cover (%)						
AF	8.3 (1.7)	8.7 (1.8)	1.2 (0.2)	0.1 (0.1)	0.0040	0.5909
C ₃ AG	2.5 (1.4)	10.0 (6.7)	0.5 (0.3)	0.3 (0.2)	0.0785	0.1995
C ₃ PG	4.5 (1.3)	14.7 (5.5)	11.6 (1.5)	23.4 (3.5)	0.1511	0.8425
C ₄ PG	48.2 (5.8)	32.4 (3.5)	49.5 (3.4)	35.4 (4.7)	0.5196	0.7985
Cactus	0.9 (0.7)	1.4 (0.8)	0.6 (0.5)	1.4 (0.8)	0.7288	0.6289
PF	4.8 (2.0)	3.1 (0.9)	1.6 (0.7)	0.9 (0.3)	0.0203	0.5469
Shrub	1.7 (1.1)	2.2 (1.1)	0.9 (0.5)	0.8 (0.3)	0.1289	0.6009

^aAF = annual forbs, C₃AG = C₃ annual grasses, C₃PG = C₃ perennial grasses, C₄PG = C₄ perennial grasses, and PF = perennial forbs.

Vegetation Responses

In agreement with our findings, previous studies from different rangeland ecosystems have largely found no changes in basal and foliar cover attributable to grazing system (e.g., Heitschmidt et al. 1987a, Hart et al. 1988, Biondini and Manske 1996, Gillen et al. 1998). However, vegetative basal cover was higher (12.4% vs. 11.6%) after 5 years with short-duration rotational grazing in a poor-condition short-grass steppe plant community (White et al. 1991). Previous research has shown that C₄ perennial grasses increase in abundance relative to C₃ perennial grasses with increasing stocking rate over long time periods (>50 years) in short-grass steppe (Hart and Ashby 1998, Milchunas et al. 1989, 1990, 1998). This pattern of species replacement is apparently initiated by selective grazing on C₃ relative to C₄ species (Hart 2001), and may be a function of the photosynthetic pathway (Caswell et al. 1973) and the greater herbivory resistance of C₄ perennial grasses, especially *B. gracilis*. Because the same stocking rate was used for the season-long continuous and the short-duration rotational grazing systems, it is not unexpected that vegetation responses were similar between grazing systems. Differences did occur with respect to bare ground and litter over the

duration of the experiment, but not between grazing systems, in response to above-average precipitation in the beginning years (1995–1999) and to conservative grazing management approaches taken during 2000 and 2002 when grazing animals were removed prior to the end of the scheduled grazing season. As a result, litter accumulated on these study pastures and, concurrently, bare ground decreased. We speculate that maintaining grazing animals on these pastures for the entire scheduled grazing seasons in 2000 and 2002 would have negated these findings because of the greater removal of vegetation by livestock and by increased hoof action.

Conclusions

Land managers in short-grass steppe who implement rotational grazing at moderate stocking rates should not expect increased livestock gains or changes in basal and foliar cover of the plant community. Livestock gains in short-grass steppe are primarily determined by stocking rate (Bement 1969), and vegetation responses are largely constrained by selection pressures of the evolutionary history of grazing and moisture, which are central to the generalized grazing model (Milchunas et al. 1988). Rotational grazing in this rangeland

ecosystem may have more utility for modifying heterogeneity of vegetation than for modifying cover or livestock production, by increasing flexibility in managing grazing pressures in paddocks within larger pastures through changes in the order of pasture use and the length of grazing periods to accommodate spatial variability in vegetation and temporal variation in precipitation. Rotational grazing could be used to help achieve conservation goals desired by society, namely, to produce goods and services through modifications of seasonality and intensity of use in paddocks within the larger management units to create heterogeneity of vegetation at much larger scales. This approach, as opposed to the traditional use of rotational grazing to promote homogeneity of use, is more consistent with historical land-use patterns that promoted biological diversity and wildlife habitat on rangelands (Fuhlendorf and Engle 2001, 2004).

ACKNOWLEDGMENTS

Mary Ashby, Jeff Thomas, Stanley Clapp, Tammy Kanode, Troy Smith, and numerous student workers collected vegetation and animal data at the Central Plains Experimental Range. Crow Valley Livestock Cooperative, Inc., provided the steers. We appreciate the insightful review comments from Robert Gillen and Patrick Reece on an earlier draft of the manuscript.

LITERATURE CITED

- BEMENT, R.E. 1969. A stocking rate guide for beef production on blue grama range. *Journal of Range Management* 22:83–86.
- BIONDINI, M.E., AND L. MANSKE. 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. *Ecological Applications* 5:239–256.
- BRUMMER, J.E., R.L. GILLEN, AND F.T. MCCOLLUM. 1988. Herbage dynamics of tallgrass prairie under short duration grazing. *Journal of Range Management* 41:264–266.
- CASSELLS, D.M., R.L. GILLEN, F.T. MCCOLLUM, K.W. TATE, AND M.E. HODGES. 1995. Effects of grazing management on standing crop dynamics in tallgrass prairie. *Journal of Range Management* 48:81–84.
- CASWELL, H., F. REED, S.N. STEPHENSON, AND P.A. WERNER. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. *American Naturalist* 107:465–480.
- DENNY, R.P., AND D.L. BARNES. 1977. Trials of multi-paddock grazing systems on veld. III. A comparison of six grazing procedures at two stocking rates. *Rhodesia Journal of Agricultural Research* 15:129–143.
- DENNY, R.P., D.L. BARNES, AND T.C.D. KENNAN. 1977. Trials of multi-paddock grazing systems on veld. I. An exploratory trial of systems involving twelve paddocks and one herd. *Rhodesia Journal of Agricultural Research* 15:11–23.
- DERNER, J.D., R.L. GILLEN, F.T. MCCOLLUM, AND K.W. TATE. 1994. Little bluestem tiller defoliation patterns under continuous and rotational grazing. *Journal of Range Management* 47:220–225.
- DERNER, J.D., H.W. POLLEY, H.B. JOHNSON, AND C.R. TISCHLER. 2004. Structural attributes of *Schizachyrium scoparium* in restored Texas blackland prairies. *Restoration Ecology* 12:80–84.
- DORMAAR, J.F., S. SMOLIAK, AND W.D. WILLMS. 1989. Vegetation and soil responses to short-duration grazing on fescue grasslands. *Journal of Range Management* 42:252–256.
- FUHLENDORF, S.D., AND D.M. ENGLE. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625–632.
- . 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41:604–614.
- GAMMON, D.M., AND B.R. ROBERTS. 1978a. Patterns of defoliation during continuous and rotational grazing of the Matopos Sandveld of Rhodesia. 1. Selectivity of grazing. *Rhodesia Journal of Agricultural Research* 16:117–131.
- . 1978b. Patterns of defoliation during continuous and rotational grazing of the Matopos Sandveld of Rhodesia. 2. Severity of defoliation. *Rhodesia Journal of Agricultural Research* 16:133–145.
- . 1978c. Patterns of defoliation during continuous and rotational grazing of the Matopos Sandveld of Rhodesia. 3. Frequency of defoliation. *Rhodesia Journal of Agricultural Research* 16:147–164.
- . 1980. Aspects of defoliation during short duration grazing of the Matopos Sandveld of Zimbabwe. *Zimbabwe Journal of Agricultural Research* 18:29–38.
- GILLEN, R.L., F.T. MCCOLLUM, AND J.E. BRUMMER. 1990. Tiller defoliation patterns under short duration grazing in tallgrass prairie. *Journal of Range Management* 43:95–99.
- GILLEN, R.L., F.T. MCCOLLUM, III, K.W. TATE, AND M.E. HODGES. 1998. Tallgrass prairie response to grazing system and stocking rate. *Journal of Range Management* 51:139–146.
- HART, R.H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. *Plant Ecology* 155:111–118.
- HART, R.H., AND M.M. ASHBY. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. *Journal of Range Management* 51:392–398.
- HART, R.H., J. BISSIO, M.J. SAMUEL, AND J.W. WAGGONER, JR. 1993a. Grazing systems, pasture size, and cattle grazing behavior, distribution and gains. *Journal of Range Management* 46:81–87.
- HART, R.H., S. CLAPP, AND P.S. TEST. 1993b. Grazing strategies, stocking rates, and frequency and intensity of grazing on western wheatgrass and blue grama. *Journal of Range Management* 46:122–126.
- HART, R.H., M.J. SAMUEL, P.S. TEST, AND M.A. SMITH. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. *Journal of Range Management* 41:282–286.

- HEFFNER, R.A., M.J. BUTLER, IV, AND C.K. REILLY. 1996. Pseudoreplication revisited. *Ecology* 77:2558–2562.
- HEITSCHMIDT, R.K., D.D. BRISKE, AND D.L. PRICE. 1990a. Pattern of interspecific tiller defoliation in a mixed-grass prairie grazed by cattle. *Grass and Forage Science* 45:215–222.
- HEITSCHMIDT, R.K., J.R. CONNOR, S.K. CANON, W.E. PINCHAK, J.W. WALKER, AND S.L. DOWHOWER. 1990b. Cow/calf production and economic returns from yearlong continuous, deferred rotation and rotational grazing treatments. *Journal of Production Agriculture* 3:92–99.
- HEITSCHMIDT, R.K., S.L. DOWHOWER, AND J.W. WALKER. 1987a. Some effects of a rotational grazing treatment on quantity and quality of available forage and amount of ground litter. *Journal of Range Management* 40:318–321.
- . 1987b. 14- vs. 42-paddock rotational grazing: aboveground biomass dynamics, forage production, and harvest efficiency. *Journal of Range Management* 40:216–223.
- HEPWORTH, K.W., P.S. TEST, R.H. HART, J.W. WAGGONER, JR., AND M.A. SMITH. 1991. Grazing systems, stocking rates, and cattle behavior in southeastern Wyoming. *Journal of Range Management* 44:259–262.
- HURLBERT, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- KHUMALO, G., AND J. HOLECHEK. 2005. Relationships between Chihuahuan desert perennial grass production and precipitation. *Rangeland Ecology and Management* 58:239–246.
- KIRBY, D.R., AND H.E. WEBB. 1986. Cattle diets on rotation and seasonlong grazing treatments. *North Dakota Farm Research* 46:14–17.
- LAUENROTH, W.K., AND O.E. SALA. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2:397–403.
- MANLEY, W.A., R.H. HART, M.J. SAMUEL, M.A. SMITH, J.W. WAGGONER, JR., AND J.T. MANLEY. 1997. Vegetation, cattle, and economic responses to grazing strategies and pressures. *Journal of Range Management* 50:638–646.
- MCCOLLUM, FT., III, R.L. GILLEN, B.R. KARGES, AND M.E. HODGES. 1999. Stocker cattle response to grazing management in tallgrass prairie. *Journal of Range Management* 52:120–126.
- MILCHUNAS, D.G., J.R. FORWOOD, AND W.K. LAUENROTH. 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. *Journal of Range Management* 47:133–139.
- MILCHUNAS, D.G., W.K. LAUENROTH, AND I.C. BURKE. 1998. Livestock grazing, animal and plant biodiversity of shortgrass steppe and relationship to ecosystem function. *Oikos* 83:64–74.
- MILCHUNAS, D.G., W.K. LAUENROTH, P.L. CHAPMAN, AND M.K. KAZEMPOUR. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11–23.
- . 1990. Community attributes along a perturbation gradient in a shortgrass steppe. *Journal of Vegetation Science* 1:375–384.
- MILCHUNAS, D.G., O.E. SALA, AND W.K. LAUENROTH. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.
- O'CONNOR, T.G., L.M. HAINES, AND H.A. SNYMAN. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology* 89:850–860.
- PITTS, J.S., AND F.C. BRYANT. 1987. Steer and vegetation response to short duration and continuous grazing. *Journal of Range Management* 40:386–389.
- SAVORY, A. 1988. *Holistic resource management*. Island Press, Covelo, CA. 564 pp.
- TEAGUE, W.R., AND S.L. DOWHOWER. 2003. Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. *Journal of Arid Environments* 53:211–229.
- VAN POOLLEN, H.W., AND J.R. LACEY. 1979. Herbage response to grazing systems and stocking intensities. *Journal of Range Management* 32:250–253.
- WHITE, M.R., R.D. PIEPER, G.B. DONART, AND L. WHITE TRIFARO. 1991. Vegetational response to short-duration and continuous grazing in south central New Mexico. *Journal of Range Management* 44:399–403.
- WOOD, M.K., AND W.H. BLACKBURN. 1984. Vegetation and soil responses to cattle grazing systems in the Texas Rolling Plains. *Journal of Range Management* 37:303–308.

Received 20 April 2006

Accepted 16 January 2007

APPENDIX. List of species by plant functional group. Nomenclature follows the USDA–NRCS Plants Database: <http://plants.usda.gov>

Plant functional group	Species
C ₃ annual grasses	<i>Vulpia octoflora</i> (Walt.) Rydb.
C ₃ perennial grasses and grass-likes	<i>Carex duriuscula</i> C.A. Mey. <i>Elymus elymoides</i> (Raf.) Swezey ssp. <i>elymoides</i> <i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth <i>Pascopyrum smithii</i> (Rydb.) A. Löve
C ₄ perennial grasses	<i>Aristida purpurea</i> Nutt. var. <i>longiseta</i> (Steud.) Vasey <i>Bouteloua dactyloides</i> (Nutt.) J.T. Columbus <i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths <i>Distichlis spicata</i> (L.) Greene <i>Muhlenbergia torreyi</i> (Kunth) A.S. Hitchc ex Bush <i>Schedonnardus paniculatus</i> (Nutt.) Trel. <i>Sorghastrum nutans</i> (L.) Nash <i>Sporobolus airoides</i> (Torr.) Torr. <i>Sporobolus cryptandrus</i> (Torr.) Gray <i>Chenopodium leptophyllum</i> (Moq.) Nutt. ex S. Wats
Annual forbs	<i>Cleome serrulata</i> Pursh <i>Cryptantha minima</i> Rydb. <i>Euphorbia glyptosperma</i> (Engelm.) Small <i>Lappula occidentalis</i> (S. Wats.) Greene var. <i>occidentalis</i> <i>Lepidium densiflorum</i> Schrad. <i>Lupinus pusillus</i> Pursh <i>Oenothera albicaulis</i> Pursh <i>Plantago patagonica</i> Jacq. <i>Polygonum aviculare</i> L. <i>Portulaca oleracea</i> L. <i>Salsola tragus</i> L.
Perennial forbs	<i>Allium textile</i> A. Nels. & J.F. Macbr. <i>Astragalus drummondii</i> Dougl. ex Hook. <i>Astragalus pectinatus</i> (Dougl. ex Hook.) Dougl. ex G. Don <i>Cirsium undulatum</i> (Nutt.) Spreng. <i>Gaura coccinea</i> Nutt. ex Pursh <i>Iva axillaris</i> Pursh <i>Lathyrus polymorphus</i> Nutt. <i>Lygodesmia juncea</i> (Pursh) D. Don ex Hook <i>Machaeranthera pinnatifida</i> (Hook.) Shinnars ssp. <i>pinnatifida</i> var. <i>pinnatifida</i> <i>Mirabilis linearis</i> (Pursh) Heimerl <i>Packera tridenticulata</i> (Rydb.) W.A. Weber & A. Löve <i>Penstemon albidus</i> Nutt. <i>Penstemon angustifolius</i> Nutt. ex Pursh <i>Phemeranthus parviflorus</i> (Nutt.) Kiger <i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb. Ex Britt. <i>Psoralidium tenuiflorum</i> (Pursh) Rydb. <i>Scutellaria brittonii</i> Porter <i>Sphaeralcea coccinea</i> (Nutt.) Rydb. <i>Thelesperma megapotamicum</i> (Spreng.) Kuntze <i>Thelesperma filifolium</i> (Hook.) Gray <i>Tradescantia occidentalis</i> (Britt.) Symth <i>Viola nuttallii</i> Pursh
Cactus	<i>Opuntia polyacantha</i> Haw.
Shrubs	<i>Atriplex canescens</i> (Pursh) Nutt. <i>Eriogonum effusum</i> Nutt. <i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby