

Drought and grazing: I. Effects on quantity of forage produced

R. K. HEITSCHMIDT, M. R. HAFERKAMP, M. G. KARL, AND A. L. HILD

Authors are supervisory rangeland scientist and rangeland scientist, USDA Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301, rangeland management specialist-ecologist, USDA Forest Service, Walla Walla, Wash. 99362, and assistant professor, Department of Rangeland Ecology and Watershed Management, University of Wyoming, Laramie, Wyo. 82071. At the time of the research, M.G. Karl and A.L. Hild were postdoctoral rangeland scientists at Fort Keogh.

Abstract

This research addresses the hypothesis that grazing intensity during and following drought can dramatically alter community level, post-drought recovery patterns. Research was conducted during the 1993 through 1996 growing seasons at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. Study plots were twelve, 5 × 10-m non-weighing lysimeters constructed in 1992 on a gently sloping (4%) clayey range site. An automated rainout shelter was constructed to control the amount of precipitation received on 6 lysimeters during the 1992 growing season. We conclude from study results that the independent and combined effects of the imposed late spring to early fall drought and associated grazing treatments were minimal relative to soil water dynamics and aboveground net primary production although both grazing treatments reduced herbage standing crops. We attribute the absence of a strong response to the drought to its timing (i.e., late growing season) in that most herbage production in these cool-season dominated grasslands is completed by early summer. Thus, annual production processes in these grasslands avoided the major impacts of the drought. The results do not provide convincing evidence, however, that would lead us to completely reject our original hypothesis. Rather, they simply provide evidence that these grasslands are well adapted to surviving late growing season drought with or without intensive grazing by ungulates.

Key Words: Primary production, species composition, standing crop, soil water

Drought is a common event in rangelands. Historically, the effects of drought on rangeland ecosystem processes have been examined by contrasting pre- and post-drought conditions in a field setting (e.g., see Albertson and Weaver 1944,

This research was conducted under a cooperative agreement between USDA-ARS and the Montana Agric. Exp. Sta. and is published as contribution no. J-5176 from the Montana Agr. Exp. Sta. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agric. Exp. Sta., or the author and does not imply its approval to the exclusion of other products that may also be suitable. USDA-Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer and all agency services are available without discrimination.

Manuscript accepted 28 Sep 1998.

Resumen

Esta investigación aborda la hipótesis de que la intensidad de apacentamiento durante y después de la sequía puede alterar dramáticamente, a nivel de comunidad, los patrones de recuperación post-sequía. La investigación se condujo durante las estaciones de crecimiento de 1993 a 1996 en el laboratorio de investigación sobre pastizales y ganado de Fort Keogh cerca de Miles, Montana. Las parcelas experimentales fueron 12 lisímetros livianos de 5 × 10 m construidos en 1992 en un sitio de pastizal arcilloso con pendiente suave (4%). Se construyó un abrigo automático protector de lluvia para controlar la cantidad de lluvia recibida en 6 lisímetros durante la estación de crecimiento de 1992. De acuerdo a los resultados del estudio, concluimos que los efectos combinados e independientes de la sequía impuesta a finales de primavera e inicio de otoño y asociada con los tratamientos de apacentamiento fueron mínimos relativo a la dinámica del agua del suelo y la producción primaria neta de la biomasa aérea, aunque ambos tratamientos de apacentamiento redujeron el forraje en pie. Atribuimos que la ausencia de una fuerte respuesta a la sequía se puede deber al tiempo en que esta ocurrió (por ejemplo, finales de la estación de crecimiento) en el que muchos de los pastos de estación fría, que son los que dominan estos pastizales, finalizan su producción de forraje a inicios del verano. En estos pastizales, los procesos de producción anual evitaron los principales impactos de la sequía. Los resultados no proveen una evidencia convincente, sin embargo, eso podría conducirnos a rechazar totalmente nuestra hipótesis original. Aun más, los resultados simplemente suministran evidencias de que estos pastizales están bien adaptados para sobrevivir a sequías que ocurren a fines de la estación de crecimiento con o sin apacentamiento intensivo de ungulados.

1946). Classic experimental designs that include appropriate non-drought control plots are uncommon. Notable exceptions are whole-plant honey mesquite (*Prosopis glandulosa*) studies by Ansley, et al. (1992) and a wide array of germplasm response studies (e.g., see Frank and Bauer 1991). The broad objective of this study was to examine the interactive effects of drought and livestock grazing on important rangeland variables in a "controlled" near natural rangeland setting.

Our fundamental hypothesis was that grazing intensities during and following drought can dramatically alter community-level, post-drought recovery patterns and that current drought and/or post-drought livestock grazing intensities tend to suppress recovery rates (Pieper and Heitschmidt 1988, Burkhardt 1996). This hypothesis stems from an underlying assumption that drought and post-drought grazing patterns of indigenous herbivores (e.g., bison) were much different than current drought and post-drought livestock grazing patterns. It seems reasonable to assume that during periods of severe drought, large herbivores: 1) suffered severely; 2) died; and/or 3) migrated out of the affected area. But assuming death or migration were dominant responses, then it can be reasoned that animal densities following drought were well below "normal" for some period of time. Although the length of this natural, post-drought "rest" period is unknown, it would have been equal to that required for the herds to either immigrate back into the affected area or repopulate the area via natality. The specific objective of this study was to examine the interaction effects of drought and varying drought and post-drought grazing regimens on herbage growth dynamics and aboveground net primary production in a northern mixed grass rangeland.

Materials and Methods

Study Area

Research was conducted during the 1993-through 1996 growing seasons at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. (46° 22'N 105° 5'W). Regional topography ranges from rolling hills to broken badlands with small intersecting streams that flow into large permanent rivers meandering through broad nearly level valleys. The potential natural vegetation on the 22,500-ha station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mixed grass dominant (Kuchler 1964). Long-term annual precipitation averages 34 cm with about 60% received during the 150-day, mid-April to mid-September growing season (Fig. 1). Average daily temperatures range from -10° C in January to 24° C in July with daily maximum

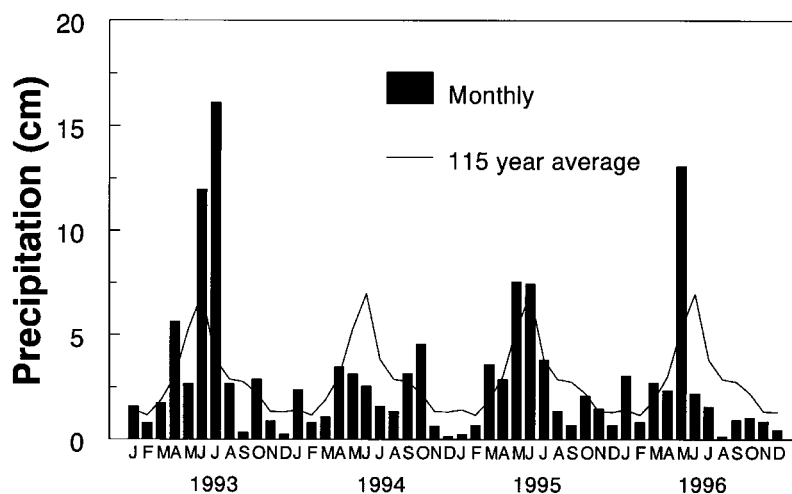


Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. (NOAA 1996).

temperatures occasionally exceeding 37° C during summer and daily minimum occasionally dipping below -40° C during winter.

Study Plots and Treatments

Study plots were twelve, 5 × 10-m non-weighing lysimeters constructed in 1992 on a gently sloping (4%) clayey range site. Lysimeters were arranged perpendicularly along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups. They were constructed by filling 12 cm wide by 2 m deep perimeter trenches, and juxtaposition aboveground 12 cm wide by 15 cm tall wooden foundations, with urethane foam insulation. Each lysimeter was equipped with 2 soil water monitoring access tubes, 1 each center upslope and down-slope. In addition, each lysimeter was equipped with a surface water runoff collection system consisting of a small (about 0.2 m²) concrete collection apron with underground plumbing for transporting water and sediment to individual fiberglass collection tanks. Lysimeter soils were Kobase silty clay loam, fine, montmorillonitic, frigid, Aridic Ustochrepts. The study area had not been grazed by livestock since 1988.

An automated rainout shelter was constructed to control amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12 × 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5 cm wide rails extending about 75 cm above the soil surface. Rails extended from top

edge (i.e., upslope) to about 15 m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associated drive system, which moved the shelter across the plots.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) graze both the year of and the year after simulated drought, hereafter referred to as the 94-95 grazed treatment; 2) graze during the year of drought and rest the year after, hereafter referred to as the 94 grazed treatment; and 3) rest both the year of and the year after drought, hereafter referred to as the ungrazed treatment. These same 3 treatments were repeated in the non-drought set of lysimeters. Plots were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995. The simulated drought was imposed from late May to mid-October 1994.

Sampling Procedures

Precipitation was monitored on site using standard rain gauges. Soil water was estimated a minimum of once a month from April through October at depths of 15, 30, 60, 90, and 120 cm using a dielectric soil water probe.

Herbage standing crop was estimated monthly by clipping ten, 250 cm² circular quadrats per lysimeter. Five quadrats each were located randomly along 2 randomly located transects, 1 in the up-

slope half of the lysimeter (i.e., up-slope) and the other in the down-slope half. Relative values of abundance were assigned to all species in each quadrat; however, only the most abundant species were clipped individually with most species combined into functionally similar groups. Species/species groups were: western wheatgrass (*Pascopyrum smithii* Rydb. (Love)), needle-and-thread grass (*Stipa comata* Trin. & Rupr.), warm-season perennial short-grasses, most of which was blue grama (*Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths), with a sprinkling of buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.); other warm-season perennial grasses of which sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) was the dominant species; *Bromus* sp. which was principally Japanese brome (*Bromus japonicus* Thunb. ex Murr.) with a small amount of downy brome (*Bromus tectorum* L.); other cool-season perennial grasses of which Sandberg's bluegrass (*Poa sandbergii* Vasey) was dominant; other cool-season annual grasses of which sixweeks fescue (*Festuca octoflora* Walt.) and little barley (*Hordeum pusillum* Nutt.) were dominant; forbs; plains pricklypear cactus (*Opuntia polyacantha* Haw.); and shrubs. Herbage was dried at 60° C for a minimum of 48 hours before weighing. Amounts of live (i.e., green) and dead (i.e., brown) tissue were then estimated by hand separation.

Data Summarization and Analyses

Herbaceous aboveground net primary production was estimated by functional group (i.e., cool-season perennial grasses, cool-season annual grasses, warm-season perennial grasses, and forbs) by summing increases in live biomass. Total herbage production was estimated by summing functional group estimates.

Data were statistically analyzed using repeated measures analysis of variance procedures. Between plot (i.e., lysimeter) effects were drought and grazing treatment. The error term for testing for these effects and their associated interactions was plot within drought and grazing treatment. Years and/or dates and all associated 2 and 3-way interactions were analyzed as within plot repeated measures and were tested using full model residuals. Mean separation procedures were least significant differ-

ence contrasts. All statistically significant differences are at $P < 0.05$.

The aboveground net primary production data were subjected to 3 different, yet closely related analyses so as to insure proper data interpretation. First, we analyzed all 4 years of the study as a single data set using the repeated measures analyses outlined above. Second, we analyzed the 1993 data separately from the 1994–1996 data using a 2-way (drought and grazing treatment) analysis of variance model for the 1993 data and the full repeated measures model described above for the 1995–1996 data set. Then to examine the potential impact of pre-treatment differences (i.e., 1993), we subtracted the 1993 production estimates from the 1994–1996 estimates and then subjected these adjusted means to the repeated measures analyses outlined above. This was determined to be the most appropriate way to identify statistically any pre-treatment differences.

Results

Precipitation and Soil Water

Amounts and patterns of annual precipitation varied widely among years (Fig. 1). During the pre-treatment year of 1993, an abundance of late spring and early summer precipitation resulted in total annual precipitation being 38% above the long-term norm of 34.1 cm. In contrast to 1993, annual precipitation during 1994 was 24.7 cm, 24% below normal, with precipitation from 1 May to 31 October, being only 16.3 cm as compared to the long-term average for this period of 27.1 cm. Total precipitation received on the drought plots during 1994 was 10.7 cm with 2.3 cm received during the months of June through October. Total annual precipitation during both the post-drought year of 1995 and the post-treatment year of 1996 was near the long-term average of 34 cm. However, patterns of distribution were quite different as the

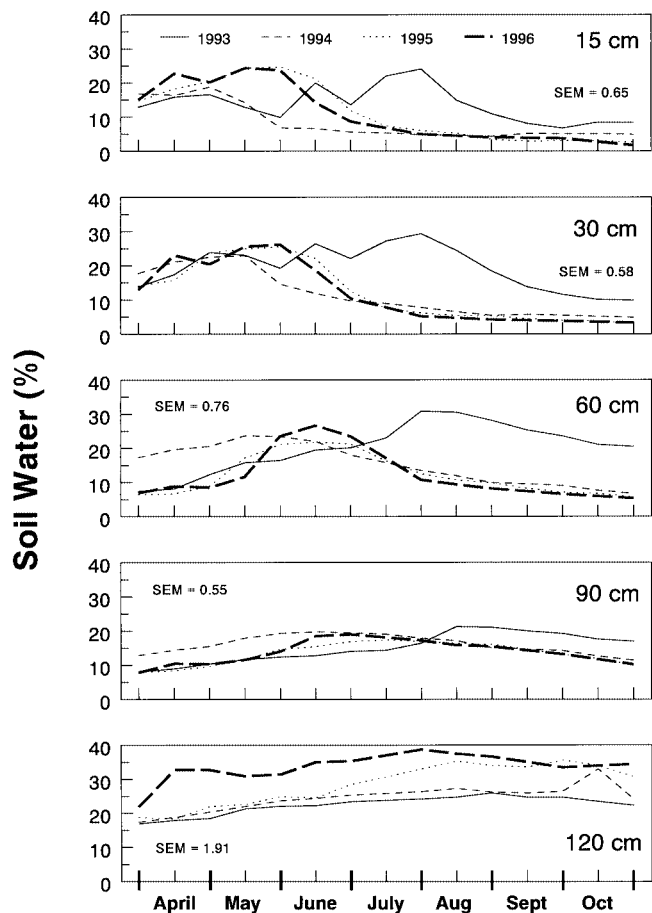


Fig. 2. Percentage soil water during the 1993 through 1996 growing seasons at 5 depths. Traces are average of the 3 grazing and 2 drought treatments as neither the main effect of grazing nor drought treatment was statistically significant.

1995 monthly pattern was similar to the long-term norm whereas the 1996 pattern was dominated by a near 200% above normal rainfall in May.

Analyses of the soil water data by depth showed impacts of the imposed 1994 drought and grazing treatments were minimal with the only statistically significant main effects being year and date. Although 32 of the 50 interaction effects included in the 5 analyses were significant, only 12 explained >2% of the variability. No definitive patterns emerged from an examination of these interactions other than the date by year interaction which was significant in all 5 depth analyses. Thus, data were combined across drought and grazing treatments for presentation (Fig. 2).

The year effect was caused by greater amounts of soil water at the 15 through 60 cm depths throughout the summer and fall of 1993 than any other year. This was largely because of the greater amount of precipitation received during June and July 1993 than other years (Fig. 1). Also, as expected, there were generally greater amounts of soil water at the 120-cm depth than the shallower depths, and magnitude of seasonal fluctuations decreased as depth of soil water increased. It is also interesting to note that soil water content at 120 cm tended to increase over the 4-year study period. We suspect this was the result of downward leakage of water around the soil water monitoring access tubes as they passed through the Kobase soil's highly impermeable clay pan located at a depth of about 1 m.

Aboveground Biomass Dynamics

Analyses of live, dead, and live + dead (i.e., total) biomass by functional group (i.e., cool-season perennial grasses, cool-season annual grasses, warm-season perennial grasses, and forbs) resulted in few significant main effects and many significant interactions. Still, interpretable, biologically meaningful patterns did emerge when standing crop data were examined within years rather than across years (Fig. 3).

In 1993, the pre-treatment year, the main effects of date and drought treatment were significant relative to total standing crop. Averaged across dates, standing crop in the grazing treatment plots allocated to the scheduled 1994 drought treatment was 2,018 kg ha⁻¹ as

compared to a 2,331 kg ha⁻¹ average for the non-drought allocated plots. This difference was largely the result of lesser amounts of cool-season perennial grasses in the drought than non-drought plots (572 vs. 1,237 kg ha⁻¹). The date effect reflected normal seasonal growth patterns (Fig. 3). The larger than normal standing crops were the result of exceptionally high rainfall (Fig. 1).

In 1994, the year the drought was imposed and the grazing treatments initiated, total standing crop was significantly altered by drought, grazing treatment, and date, and by the interaction of grazing treatment by date. The significant grazing treatment by date interaction resulted from the effects the early June and July grazing events had on

standing crops during the remainder of the year (Fig. 3). For example, averaged across the 2 drought treatments, total standing crop from July through October was about 2,000 kg ha⁻¹ less in the 8 grazed than 4 ungrazed treatment plots following average declines of 1,387 and 778 kg ha⁻¹ during the June and July grazing events, respectively. The significant drought effect arose because average standing crop in the drought treatments was 1,735 kg ha⁻¹ as compared to 2,084 kg ha⁻¹ in non-drought treatments. Averaged across dates, standing crop in the 2 grazed treatments averaged 1,580 kg ha⁻¹ as compared to 2,567 kg ha⁻¹ in the ungrazed treatment. The date effect was again the result of normal seasonal growth dynamics.

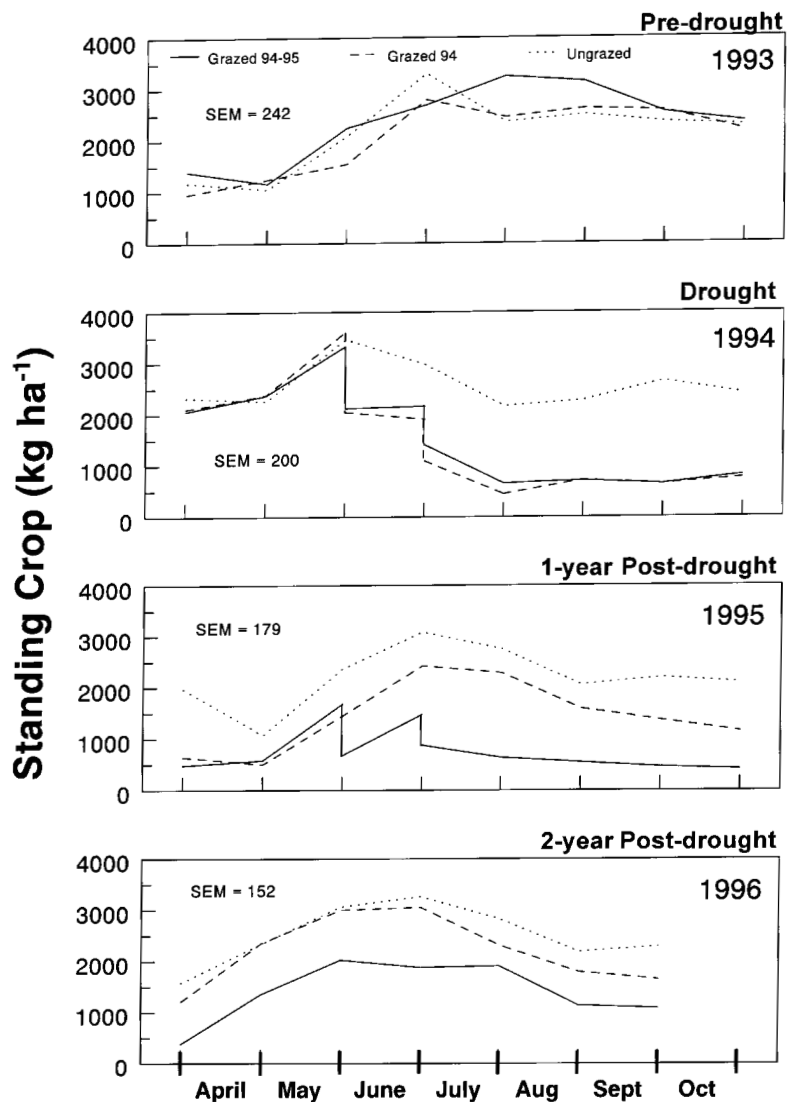


Fig. 3. Herbage standing crops (kg ha⁻¹) for the 3 grazing treatments during the 1993 through 1996 growing seasons. Traces are average of 2 drought treatments.

In 1995, the first post-drought recovery year, total standing crop was again significantly altered by the main effects of the 1994 drought, grazing treatment, and date, and by the interaction of grazing treatment and date. However, the grazing treatment by date interaction was more complex than in 1994 in that in the early portion of the growing season it was the result of both 1994 grazing treatments whereas in the latter part of the season it was largely the result of just the 94-95 grazing treatment (Fig. 3). Again, average standing crop in the 1994 drought plots was less than in non-drought plots (1,259 vs. 1,673 kg ha⁻¹) and, as expected, varied significantly among grazing treatments being least in 94-95 grazed (782 kg ha⁻¹) and greatest in the ungrazed (2,196 kg ha⁻¹) with 94 grazed intermediate (1,422 kg ha⁻¹). The date effect was, as in previous years, the result of normal seasonal growth dynamics.

In 1996, the second post-drought recovery year and the first wherein no plots were grazed regardless of previous treatment, only the main effects of grazing treatments and date were significant. The grazing treatment effect arose because average standing crop of 1,398 kg ha⁻¹ in the 94-95 treatment was significantly less than the 2,353 kg ha⁻¹ average for the 94 grazed and the ungrazed treatment. There was no difference between the 94 grazed and the ungrazed treatments. Date effects were, as in previous years, a reflection of normal seasonal growth dynamics (Fig. 3).

Aboveground Net Primary Production

Results from the analyses of the adjusted production data (i.e., 1993 means subtracted from 1994-1996 means) supported the data interpretation arising from the analyses of the unadjusted means. The only difference between the 2 analyses was that the main effects of drought treatment on total, cool-season perennial grass, and annual grass production was significant ($P < 0.05$) in the analyses of the unadjusted means but not the adjusted means ($P > 0.18$). The main effects of year and all interaction effects were identical. Insights arising from these differences are duly noted in the presentation of results below.

Analyses of the 1993 production data showed there were no differences among

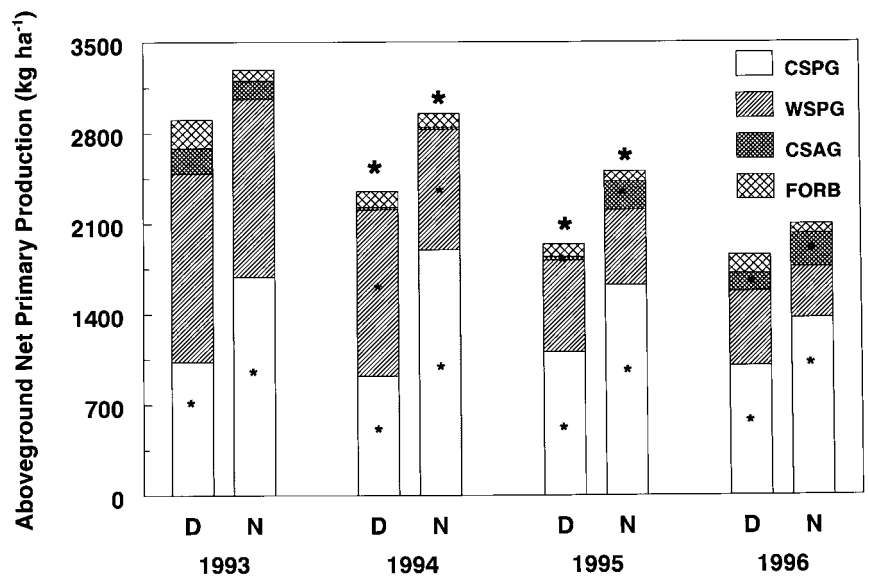


Fig. 4. Aboveground net primary production estimates (kg ha⁻¹) for drought (D) and non-drought (N) treatments for 1993 through 1996. Species groups within a year with asterisks are significantly different @ $P < 0.05$. Totals within a year with asterisk above column at significantly different @ $P < 0.05$.

plots in total production averaging 3,097 kg ha⁻¹. However, some differences among plots were found in cool-season perennial grass and forb production (Fig. 4). Cool-season grass production was less in plots allocated for the 1994 drought treatment than non-drought plots (1,030 vs. 1,687 kg ha⁻¹) largely because of less western wheatgrass in drought than non-drought plots. Forb production in the drought 94-95 grazing treatment was several fold greater than all other grazing treatment plots (580 vs. 66 kg ha⁻¹). This was largely because we harvested 18 g of forbs from 1 of the 10 randomly located 250 cm² sample quadrat (i.e., 1,434 kg ha⁻¹) on 1 date in 1 of the two, 94-95 grazed treatment plots. As a result, forb production averaged 580 kg ha⁻² in the drought 94-95 grazed treatment as compared to only 66 kg ha⁻² in the 5 other treatments.

Analyses of total production (i.e., sum of functional groups) from 1994 through 1996, showed significant drought and year effects with no interactions. Averaged across years and grazing treatments, total production in drought plots was 2,049 kg ha⁻¹ as compared to 2,518 kg ha⁻¹ in non-drought plots. The primary difference between the drought and non-drought plots was in amounts of cool-season perennial grasses (1,009 vs. 1,629 kg ha⁻¹) (Fig. 4). However, this difference was a carryover of pretreatment differ-

ences in production rather than the imposed 1994 drought. This was confirmed by the loss of significant drought treatment effects on total and cool-season perennial grass production when 1994-1996 means were adjusted by subtracting 1993 means. There was also less annual grass production in drought (61 kg ha⁻¹) than non-drought plots (164 kg ha⁻¹) depending upon year. But again, this was largely because of pre-treatment differences in annual grass production.

Surprisingly, total production was greater during the drought year of 1994 than the 2 post-drought years of 1995 and 1996. Averaged across drought and grazing treatments, production averaged 2,651 kg ha⁻¹ in 1994 as compared to an average of 2,100 kg ha⁻¹ in 1995 and 1996 (Fig. 4). These differences were largely the result of a significant decline in warm-season perennial grass production from 1994 through 1996 which averaged 1,110, 645, and 486 kg ha⁻¹, respectively. On the other hand, there was a significant increase in cool-season annual grass production from 17 kg ha⁻¹ in 1994 to 197 kg ha⁻¹ in 1996. Annual grass production in 1995 was intermediate to 1994 and 1996 averaging 123 kg ha⁻¹.

Although grazing treatment was not significant in any of the herbage production analyses, there were 2 significant year by grazing treatment effects. The first was warm-season grass production

Table 1. Two-way interaction effects of year and grazing treatment on aboveground net primary production (kg ha⁻¹) of warm-season perennial grasses. Means are averaged across drought treatments.

Year	Grazing Treatments		
	94-95	94	ungrazed
	----- (kg ha ⁻¹) -----		
1994	1,220 ¹ _a	1,329 _a	781 _b
1995	675 _b	559 _b	701 _b
1996	384 _c	455 _{bc}	619 _{bc}

¹Means in a row or column followed by same letter are not significantly different at P=0.05.

(Table 1) in which the annual production pattern indicated grazing reduced warm season grass production regardless of drought treatment. The second year by grazing treatment interaction effect was cool-season annual grass production (Table 2). In this instance, it appeared that grazing during drought had no effect on production whereas grazing the year after drought tended to decrease annual grass production.

Discussion and Conclusions

Previous research on Northern Great Plains rangelands has shown generally that grazing is a secondary factor affecting ecosystem processes whereas drought is a primary factor (Whitman et al. 1943, Hurt 1951, Reed and Peterson 1961, Olson et al. 1985, Biondini and Manske 1996, Biondini et al. 1998). Our results support this conclusion well with regards to grazing impacts but not as it relates to drought. Quite honestly, the imposed drought did not impact the variables we examined to the extent hypothesized. Evidence supporting this conclusion are that the independent and combined effects of the imposed drought and grazing treatments were minimal relative to soil water dynamics (Fig. 2) and aboveground net primary production (Fig. 4). Granted, grazing treatments did reduce herbage standing crops (Fig. 3), but that was as expected.

We believe the primary reason the drought in this study had minimal impact on post-drought recovery patterns is most likely related to timing of the drought (i.e., late growing season). These grasslands are dominated by cool-season plant species that complete most of their growth by late spring and early summer (Heitschmidt et al. 1995, Dodd et al. 1982); thus, plants only need suffi-

cient amounts of soil water until late spring to complete their "normal" production cycle. In this study, there was apparently a sufficient soil water reserve when the drought was initiated (i.e., late May, see Fig. 2) for the annual production cycle to be completed. A compounding factor that may have dampened our ability to detect drought effects, was that the amount of ambient precipitation falling on non-drought plots during the imposed drought was well below normal (Fig. 1). Thus, late season production on non-drought plots may have been curtailed by natural drought although magnitude of curtailment did not appear to be great since annual production in 1994 was similar to 1995 and 1996 (Fig. 4).

The positive effect that the 1994 drought had on warm-season grass production (Fig. 4) was unexpected. Logically, one would assume that a late spring drought would depress production of warm-season species more than cool-season species. We offer no explanation for these results.

The general absence of grazing treatment effects on primary production was also unexpected although in retrospect we believe timing of drought greatly dampened the interaction of drought and grazing treatment. An exception was warm-season perennial grass production wherein grazing during the 1994 drought appeared to initiate a declining post-drought production trend regardless of post-drought grazing treatment (Table 1). We hypothesize this was because our June and July flash grazing tactics somehow enhanced warm-season grass growth. But since this was not manifested in 1995 in the 94-95 grazed treatment, definitive conclusions as to causal factors for the 1994 results are difficult.

We hypothesize that the causal factors associated with the interaction of year and grazing treatment on annual grass production (Table 2) were most likely related to both climatic growing conditions and the impacts that level of ground cover has been shown to have on Japanese brome production in other regions (Whisenant 1990, Heitschmidt et al. 1982). However, there was no clear evidence supporting any single explanation; thus, we choose to limit our speculation.

The results of this study also provide strong support for the need for pre-treatment baseline data in field studies. For example, consider what conclusions

Table 2. Two-way interaction effects of year and drought treatment on aboveground net primary production (kg ha⁻¹) of annual grasses. Means are averaged across drought treatments.

Year	Grazing Treatments		
	94-95	94	ungrazed
	----- (kg ha ⁻¹) -----		
1994	23 ¹ _a	10 _a	18 _a
1995	150 _b	123 _b	98 _{ab}
1996	110 _{ab}	239 _c	244 _c

¹Means in a row or column followed by same letter are not significantly different at P=0.05.

might have been drawn from the results without pre-treatment data. The most obvious conclusions would have been that the drought depressed total herbage production substantially, even up to 2 years after the drought and that the major contributing factor was a substantial reduction in cool-season perennial grass production. However, inclusion of the 1993 data in our interpretation dampens greatly the magnitude of the effect of the drought on both total production and functional group's contributions to the total.

And lastly, the results from this study's non-drought, ungrazed plots are very similar to findings from similar studies conducted on indigenous Northern Great Plains rangelands in terms of seasonal growth dynamics and productivity capacity (Lewis et al. 1971, Coupland 1974, Laurenroth et al. 1975, Lauenroth and Whitman 1977, Sims and Singh 1978a, 1978b, Dodd et al. 1982, Singh et al. 1983, Heitschmidt et al. 1995). Normally, peak standing crop in the Northern Great Plains occurs between early June and mid-July depending upon plant species composition and pattern and amount of precipitation. Our data fit this pattern well (Fig. 3). Similarly, estimated aboveground herbage production for this region ranges between 1,600 and 4,000 kg ha⁻¹ depending upon site, year, and methodology (Singh et al. 1983, Heitschmidt et al. 1995, Biondini and Manske 1996, Biondini et al. 1998). The results of this study support these generalizations well (Fig. 4).

Literature Cited

- Albertson, F.W. and J.F. Weaver. 1944.** Effects of drought, dust, and intensity of grazing on cover and yield of short-grass pastures. *Ecol. Monogr.* 14:1-29.

- Albertson, F.W. and J.F. Weaver. 1946.** Reduction of ungrazed mixed prairie to short grass as result of drought and dust. *Ecol. Monogr.* 16:449-463.
- Ansley, R.J., P.W. Jacoby, C.H. Meadors, and B.K. Lawrence. 1992.** Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). *J. Arid Envir.* 22:147-159.
- Biondini, M.E. and L. Manske. 1996.** Grazing frequency and ecosystem processes in a northern mixed prairie. *Ecol. Appl.* 6:239-256.
- Biondini, M.E., B.D. Patton, and P.E. Nyren. 1998.** Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecol. Appl.* 8(2):469-479.
- Burkhardt, J.W. 1996.** Herbivory in the Intermountain West. Idaho Forest, Wildl. Range Exp. Sta. Bull. 58. Moscow, Ida.
- Coupland, R.T. 1974.** Producers: VI. Summary of studies of primary production by biomass and shoot observation methods. Can. Comm. IBP. Matador Proj. Tech. Rep. No. 62. Univ. Sask. Saskatoon, Sask.
- Dodd, J.L., W.K. Lauenroth, and R.K. Heitschmidt. 1982.** Effects of controlled SO₂ exposure on net primary production and plant biomass dynamics. *J. Range Manage.* 35:572-579.
- Frank, A.B. and A. Bauer. 1991.** Rooting activity and water use during vegetative development of crested and western wheatgrass. *Agron. J.* 83:906-910.
- Heitschmidt, R.K., E.E. Grings, M.R. Haferkamp, and M.G. Karl. 1995.** Herbage dynamics on 2 Northern Great Plains range sites. *J. Range Manage.* 48:211-217.
- Heitschmidt, R.K., D.I. Price, R.A. Gordon, and J.R. Frasure. 1982.** Short duration grazing at the Texas Experimental Ranch: Effects on above-ground net primary production and seasonal growth dynamics. *J. Range Manage.* 35:367-372.
- Hurt, L.C. 1951.** Managing northern Great Plains cattle ranges to minimize the effects of drought. USDA Circ. #865.
- Kuchler, A.W. 1964.** Potential natural vegetation of the conterminous United States. *Amer. Geogr. Soc. Spec. Pub.* 36, New York, N.Y.
- Lauenroth, W.K. and W.C. Whitman. 1977.** Dynamics of dry matter production in a mixed-grass prairie in western North Dakota. *Oecologia (Berl.)* 27:339-351
- Lauenroth, W.K., J.L. Dodd, R.K. Heitschmidt, and R.G. Woodmansee. 1975.** Biomass dynamics and primary production in mixed prairie grasslands in southeastern Montana: Baseline data for air pollution studies, p. 559-578. In: Proc. Fort Union Coal Field Symp. Mont. Acad. Science. Billings, Mont.
- Lewis, J.K., J.L. Dodd, H.L. Hutcheson, and C.L. Hanson. 1971.** Abiotic and herbage dynamics studies on the Cottonwood Site, 1970. US/IBP Grassland Biome Tech. Rep. No. 111, Colorado State Univ., Ft. Collins, Colo.
- National Oceanic and Atmospheric Administration. 1996.** Climatological data, Montana annual summary. Nat. Climatol. Data Center, Asheville, N.C.
- Olson, K.C., R.S. White and B.W. Sindelar. 1985.** Responses of vegetation of the northern great plains to precipitation amount and grazing intensity. *J. Range Manage.* 38:357-361.
- Pieper, R.D. and R.K. Heitschmidt. 1988.** Is short-duration grazing the answer? *J. Soil and Water Conserv.* 43(2):133-137.
- Reed, M.J. and R.A. Peterson. 1961.** Vegetation, soils, and cattle responses to grazing on northern Great Plains range. USDA For. Serv. Tech. Bull. #1252.
- Sims, P.L. and J.S. Singh. 1978a.** The structure and function of ten western North American grasslands II. Intra-seasonal dynamics in primary producer compartments. *J. Ecol.* 66:547-572.
- Sims, P.L. and J.S. Singh. 1978b.** The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *J. Ecol.* 66:573-597.
- Singh, J.S., W.K. Lauenroth, R.K. Heitschmidt, and J.L. Dodd. 1983.** Structural and functional attributes of the vegetation of northern mixed prairie of North America. *Bot. Rev.* 49:117-149.
- Whisenant, S.G. 1990.** Postfire population dynamics of *Bromus japonicus*. *Amer. Midl. Natur.* 123:301-308.
- Whitman, W., H.C. Hanson and P.A. Peterson. 1943.** Relation of drought and grazing to North Dakota rangelands. *North Dakota Agr. Exp. Sta. Bull.* #320.