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# Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing

Richard H. Hart, Rangeland Scientist
*High Plains Grasslands Research Station, US Dept. of Agriculture, Agricultural Research Service, 8408 Hildreth Road, Cheyenne, WY 82009, USA; *Author for correspondence*

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## Abstract

Shortgrass steppe rangeland near Nunn, Colorado, USA, has been lightly, moderately, or heavily grazed by cattle, or protected from grazing in exclosures, for 55 years. Plant species biodiversity and evenness were greatest in lightly- and moderately-grazed pastures. Both pastures were dominated by the warm-season shortgrass *Bouteloua gracilis*, but the cool-season midgrasses *Pascopyrum smithii* and *Stipa comata* contributed significantly to biomass production on the lightly-grazed pasture, as they did in the exclosures. Diversity was least in the exclosures, which were strongly dominated by the cactus *Opuntia polyacantha*. *Buchloë dactyloides*, another warm-season shortgrass, and *Bouteloua gracilis* were co-dominants under heavy grazing, and diversity was intermediate. Plant community structure and diversity were controlled by selective grazing by cattle and soil disturbance by cattle and rodents. Shortgrass steppe moderately or heavily grazed by cattle was similar to and probably as sustainable as steppe grazed for millenia by bison and other wild ungulates.

## Introduction

Light to moderate levels of grazing usually result in a richer diversity of plant species than do heavy levels of grazing or no grazing at all, expecially in the more humid grasslands such as the tall-grass prairie in the United States (Risser et al. 1981). Moderate grazing by bison increased plant biodiversity on tallgrass (Collins et al. 1998; Hartnett et al. 1996), and moderate grazing by cattle increased plant biodiversity on tallgrass (Collins 1987), mixed-grass prairie (Biondini et al. 1998), and shortgrass steppe (Milchunas et al. 1990, 1992). On the other hand, very heavy grazing that removed 90% of above-ground biomass reduced diversity on mixed-grass prairie (Biondini et al. 1998). Grazing increased nitrogen concentration in topsoil (Schuman et al. 1999), accelerated recycling of nitrogen (Hobbs et al. 1991; McNaughton et al. 1997), and created intermediate levels of disturbance (Milchunas et al. 1988; Hobbs and Huenneke 1992). These effects have been proposed as the mechanisms whereby grazing increases biodiversity at landscape and smaller scales.

A study at the Central Plains Experimental Range (CPER) provided an unique opportunity to examine the long-term effects of protection from grazing and grazing at different intensities on plant community composition and biodiversity. The CPER is about 20km northeast of Nunn, Colorado and 50km southeast of Cheyenne, Wyoming, USA, at about 104°40′ W and 40°40′ N. Total annual precipitation ranged from 130 to 500 mm over the course of this grazing study, with 50 to 80% falling in May through September. Soils in the study area were mostly sandy loams, with smaller areas of loams and clay loams.

Vegetation is dominated by the warm-season shortgrasses *Bouteloua gracilis* (H.B.K.) Lag. ex Steud and *Buchloë dactyloides* (Nutt.) Engelm., and the warm-season midgrass *Aristida longiseta* (Steud.) Vasey (Table 1). The cool-season midgrasses *Pascopyrum smithii* (Rydb.) A. Love and *Stipa comata* Trin. & Rupr. make up a small but significant component of the vegetation; other graminoids include *Carex eleocharis* Bailey, *Elymus elymoides* (Raf.) Swezey, and *Sporobolus cryptandrus* (Torr.) Gray. The cactus *Opuntia polyacantha* Haw. is extremely abundant. *Artemisia frigida* Willd. is a common suffrutescent, and

*Table 1.* Biomass, as percent of total, of major plant species on shortgrass steppe rangeland after 55 years of zero, light, moderate, or heavy grazing.

| | Grazing intensity | | | |
|---|---|---|---|---|
| Species or group | Zero | Light | Moderate | Heavy |
| *Aristida longiseta* (Steud.) Vasey | 4.41 | 8.14 | 14.80 | 8.14 |
| *Artemisia frigida* Willd. | 12.34 | 18.58 | 5.84 | 0.00 |
| *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. | 15.29 | 37.65 | 40.87 | 34.04 |
| *Buchloë dactyloides* (Nutt.) Engelm. | 0.50 | 2.54 | 7.74 | 22.09 |
| *Opuntia polyacantha* Haw. | 48.38 | 18.04 | 15.55 | 22.48 |
| *Pascopyrum smithii* (Rydb.) A. Love | 4.29 | 0.83 | 2.66 | 0.79 |
| *Stipa comata* Trin. & Rupr. | 7.26 | 2.00 | 0.03 | 0.13 |
| Other graminoids | 3.30 | 5.79 | 3.84 | 5.94 |
| Shrubs & suffrutescents | 1.23 | 3.77 | 3.98 | 1.36 |
| Forbs | 2.98 | 2.65 | 4.69 | 5.03 |

*Sphaeralcea coccinea* (Nutt.) Rydb. is the most common perennial forb.

## Methods

In 1939, grazing began on 4 replications of a grazing intensity study at the CPER, but no data were taken until 1940. Botanical composition in all pastures and exclosures of this grazing study was very similar in 1940–1942 (Klipple and Costello 1960). Between 1950 and 1978, replicates were removed from the system until only a single pasture, of approximately 128 ha, remained at each intensity. Pastures were grazed each year by yearling Hereford heifers. From 1940 through 1964, light, moderate, and heavy grazing pastures were stocked and grazed to remove 20, 40, and 60%, respectively, of the current year's growth of grasses during a 6-month grazing season, May through October. From 1965 through 1994, light, moderate, and heavy grazing were stocked to leave a total of 500, 335, and 225 kg $ha^{-1}$ of ungrazed herbage at the end of the grazing season. Cattle gain data were reported by Hart and Ashby (1998).

In 1993 and 1994, detailed measurements of peak standing crop (PSC) of above-ground biomass were made on the remaining replication. Sixty permanent, systematically spaced, 1.5 × 1.5 m cages were located in each pasture. Cages were moved a few meters each spring before plant growth started. In addition, 20 permanent 1.5 × 1.5 m plots were located in a 0.4- to 0.8-ha permanent exclosure in each pasture, for a total of 60 plots, ensuring that the same number of cages/plots were sampled at all four intensities. Biomass of every plant species was estimated at approximately peak standing crop by the micro-unit forage inventory method (Shoop and McIlvain 1963), a double-sampling technique using clipping and ocular estimation, in two 30 × 60 cm quadrats per pasture cage or exclosure plot. Every fifth quadrat was clipped and estimated., and regressions of clipped weights of each species on estimated weights were calculated. In no case was the slope of the regression line significantly different from 1, indicating that the technique was a reliable estimator of biomass of all species.

Biomass is the best parameter for estimating plant biodiversity in grasslands (Guo and Rundel 1997). It is not possible to use density (number of individuals per unit area) because it is impossible to identify individuals of stoloniferous species such as *B. dactyloides* or rhizomatous species such as *P. smithii*. Also, only a fraction of an individual bunchgrass plant may be included in a sampling unit.

All calculations are based on data from 120 quadrats in 60 cages or plots; data from the three exclosures under zero grazing were pooled. Obviously, not all species in any 128-ha pasture were found in the quadrats. The total number of species in a pasture was estimated from the negative correlation between species rank and the logarithm of the percentage of plots in which that species occurred; $r^2 = 0.92$ to 0.96. Within each plot, an area of 0.36 $m^2$ was harvested; 3,555,556 such areas would totally cover a 128-ha pasture. From the regressions of species rank on log frequency, the rank of the species which would occur only once in a 128-ha pasture or exclosure, equal to a frequency of 1/3,555,556, was calculated. If, for example, it was calculated that the 99th-ranking species

*Table 2.* Number of plant species and evenness, diversity and dominance indices on shortgrass steppe rangeland after 55 years of zero, light, moderate, or heavy grazing.

| Grazing intensity | Number of plant species | | Shannon and Weaver (1949) | | Simpson (1949); Pielou (1966) | |
|---|---|---|---|---|---|---|
| | Found in quads | Calculated present in 128-ha pastures | Evenness | Diversity | Diversity | Dominance |
| Zero (exclosures) | 46 a | 99 | 0.465 c | 0.714c | 3.68b | 0.282a |
| Light | 36 c | 71 | 0.557 a | 0.762b | 4.63a | 0.219b |
| Moderate | 46 ab | 103 | 0.535ab | 0.836a | 4.33a | 0.225b |
| Heavy | 43 b | 97 | 0.500bc | 0.726c | 4.56a | 0.223b |

a, b Parameters in the same column, followed by the same letter, do not differ at the 0.05 level.

was the rarest species, occurring only once in the pasture, it follows that 99 species were present in the pasture.

Diversity, evenness, and dominance indices (Simpson 1949) were calculated from biomass production of each plant species, expressed as a per cent of total production. Measurements of biodiversity must address both richness, the number of species in a community, and evenness or dominance, the relative abundances of the species. Differences in relative abundance imply differences in dominance, but dominance, as indicated by greater numbers of individuals or biomass of a particular species, may or may not be a reflection of importance to ecosystem function (West and Whitford 1995).

A jack-knifing procedure was used to calculate "pseudo-values" for estimates of species richness (Heltshe and Forrester 1983) and diversity, evenness, and dominance (Magurran 1988). The pseudo-values were subjected to analyses of variance to obtain pooled estimates of variance. Differences among means were identified by *t*-test.

## Results

From 43 to 46 plant species were found under zero, moderate, and heavy grazing, but only 36 were found under light grazing (Table 2), more species than were found at a single sampling date in previous studies on shortgrass steppe (Lauver 1997; Risser 1971). The correlation between species rank and frequency of occurence provided an estimate of the total number of plant species in the pasture; 97 to 103 under zero, moderate, and heavy grazing, but only 71 under light grazing (Table 2). Thus species richness was greatly reduced under light grazing as compared to the other three intensities.

Singh et al. (1996) sampled the same moderately-grazed pastures that we sampled, and calculated that the number of plant species increased with the logarithm of the area. Their equations, excluding data from one species-poor site, predict from 82 to 115 species would be found if the entire pasture was sampled. This agrees well with our estimate of 103 species, which was also the total number of species found by Singh et al. (1996) in the seventeen 40 × 40 m plots that they sampled.

Evenness, dominance, and diversity indices agreed that plant communities in the zero-grazed exclosures were less diverse, the contributions of the different species to total biomass were more unequal (lower evenness), and the level of dominance higher, reflecting the overwhelming influence of *O. polyacantha*. Simpson's indices showed no significant differences in dominance and diversity among light, moderate, and heavy grazing. Shannon's indices indicated that the heavily-grazed pastures included less diverse plant communities than the lightly- or moderately-grazed pastures, and the distribution of biomass among species was less even than on the lightly-grazed pasture.

The lower diversity under zero grazing reflects the overwhelming dominance of *Opuntia polyacantha*, which provided 48% of the biomass under zero grazing (Table 1), but only 16 to 22% under light to heavy grazing. In 1969, the frequency of *O. polyacantha* was higher in the exclosure and under light grazing than under moderate or heavy grazing (Fisser et al. 1969), but plants tended to be smaller than in the heavy-grazed pasture, resulting in a lower biomass. However, under zero grazing the small *O. polyacantha* of 1969 had grown by 1993–1994 into large ones, and the species totally dominated the plant community. No other plant species approached this level of dominance under any treatment. Standing crop of *O. polyacantha*, unlike that of the other species, includes some biomass from previous growing seasons, but this is true under all four intensities so does not affect its relative rank among intensities.

*Bouteloua gracilis*, the second most common species, provided 34 to 41% of biomass under grazing but only 15% under zero grazing. *Buchloë dactyloides* was common only under heavy grazing, producing 22% of the total biomass. *Artemisia frigida* was most common under zero or light grazing, 12 and 19% respectively, and *Aristida longiseta* was most common under moderate grazing, 15%.

## Discussion

Selective grazing by large ungulates is considered to be the major cause of shifts in rangeland plant communities (Anderson and Briske 1995). We found that *B. gracilis* and *B. dactyloides* increased relative to the preferred grasses *P. smithii* and *S. comata* as grazing intensity increased. At CPER (Vavra et al. 1977), cattle consumed 16 and 32% of available *B. gracilis* under light and heavy grazing, respectively, and 38 and 28% of *B. dactyloides*, vs. 88 and 97% of *P. smithii* and 75% and 100% of *S. comata*.

Selectivity may change with grazing intensity. At CPER, cattle consumed only 2% of the available *Artemisia frigida* under light grazing, but 72% under heavy grazing, and 7% of available *A. longiseta* under light grazing but 88% under heavy grazing (Vavra et al. 1977). We found that *A. frigida* disappeared under heavy grazing but made up 19% of biomass under light grazing. *Aristida longiseta* is expected to increase under heavy grazing, but we found only about half as much *A. longiseta* under heavy grazing as under moderate grazing.

The explosive increase of *O. polyacantha* under zero grazing likely reflects, not a release from selective grazing by cattle, but a release from trampling, which allowed the small *O. polyacantha* plants between the old, dense clumps to survive and grow. Grazing may have increased temperature and dryness of surface soil, making it difficult for seedling cactus to establish and survive between established clumps (Fisser et al. 1969).

Milchunas et al. (1990) stated "…the lack of grazing (on the same pastures used in our study) promoted species characteristic of disturbances," and disturbances by rodents appeared to be more frequent in the ungrazed exclosures. Soil disturbance, herbivory, and granivory by rodents may have been necessary to open up sites for establishment of uncommon species in the zero-grazed exclosures (Archer et al. 1987; Brown and Heske 1990; Hansen and Gold 1977; Weltzin et al. 1997). Milchunas et al. (1992) seeded several weedy annual forbs into grazed and ungrazed shortgrass steppe; none became established in the grazed areas, but enough *Kochia scoparia* (L.) Schrad. and *Salsola iberica* Sennen & Pau became established in the ungrazed areas to significantly increase the density of these species.

Fire may interact with grazing to increase biodiversity on tallgrass prairie (Collins 1987; Collins et al. 1998; Hartnett et al. 1996) or *Juniperus-Quercus* savanna (Fuhlendorf and Smeins 1997), but probably has less effect on shortgrass steppe (Wright and Bailey 1980).

A number of workers have concluded that biodiversity increases the stability and productivity of ecosystems (Tilman et al. 1997). Others have found no increase in total production with increased diversity, and ecosystems such as Fraser fir forest and some heath balds function very well with only a few species of vascular plants and low plant species diversity (Whittaker 1965). At CPER, species richness was the same in ungrazed and moderately grazed communities, and diversity was higher in the moderately grazed community. Nonetheless, peak standing crop of above-ground biomass was 1355 $kg\,ha^{-1}$ on the ungrazed community vs. 730 $kg\,ha^{-1}$ on the moderately grazed community. Much of the difference was caused by the large standing crop of *O. polyacantha*, which included some production from previous years, on the ungrazed community, but total production minus *O. polyacantha* was still higher on the ungrazed community, 700 vs. 615 $kg\,ha^{-1}$. Cumulative effects of 55 years of grazing were manifested in reduced biomass production, independent of plant biodiversity.

Diversity of services, processes, and disturbances within ecosystems may be more important than diversity of species on rangelands (West and Whitford 1995). All species are not equally important to the function of an ecosystem. American chestnut trees (*Castanea dentata* Borkh.) and passenger pigeons (*Ectopistes migratorius* L.), formerly species of major importance in the eastern deciduous forests of the US, were removed from this ecosystem in the 20th century. After a short period of adjustment, other species assumed the function of chestnuts and pigeons, and productivity and watershed protection were unchanged (Johnson and Mayeux 1992). On the other hand, consequences were severe for the seven species of Lepidoptera that fed exclusively on chestnut and therefore became extinct. We have no way of knowing the possible evolutionary consequences of the loss of chestnuts, pigeons, and seven species of butterflies and moths. Preservation of species may have biological and aesthetic value regardless of biodiversity.

Large herbivores play a crucial role in the maintenance of diverse communities of plants, birds, and invertebrates associated with grasslands (Larson 1940). Local diversity of prey species may be related to the number of predators in the system and their ability to prevent any one prey species from monopolizing some limiting factor (Paine 1966). Grazers bear the same relationship to plant species as predators do to prey species, and should have similar impacts on species diversity. In addition, grazers hasten the recycling of nutrients and create local disturbances that provide niches for many plant species.

Although grazing maintains or increases diversity, different plant species, both dominant and rare, occur in grazed and ungrazed ecosystems. Maintaining ungrazed ecosystems as well as ecosystems grazed at different intensities will produce greater landscape diversity in both plant species and the animal species that depend upon them for food and habitat. The aspect of the shortgrass steppe before European settlement, as described in the journals of early visitors to the Great Plains, was very similar to that of the heavily-grazed pastures (Hart and Hart 1997). Such observations indicate that the plant communities of the shortgrass steppe are a true climax, not a grazing disclimax, which evolved under moderate to heavy grazing by bison (*Bison bison* L.; Larson (1940)). They should be sustainable under moderate to heavy grazing by cattle, whose diet is very similar to that of bison. Although behavior of the two species differs somewhat (Plumb and Dodd (1993), rangelands appear to be sustainable under optimum management for each species.

## Appendix

*Table A1.* Biomass, as percent of total, of plant species found on shortgrass steppe rangeland after 55 years of zero, light, moderate, or heavy grazing.

| | | Grazing intensity | | | |
|---|---|---|---|---|---|
| Scientific name | Common name | Zero | Light | Moderate | Heavy |
| *Aristida longiseta* (Steud.) Vasey | Red threeawn | 4.410 | 8.138 | 14.800 | 8.140 |
| *Artemisia frigida* Willd. | Fringed sagewort | 12.344 | 18.581 | 5.842 | 0.000 |
| *Astragalus* spp. | Milkvetch | 0.000 | 0.010 | 0.052 | 0.039 |
| *Astragalus mollisssimus* Torr. | Wooly milkvetch | 0.000 | 0.092 | 0.000 | 0.122 |
| *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. | Blue grama | 15.290 | 37.651 | 40.870 | 34.043 |
| *Bromus tectorum* L. | Cheatgrass brome | 0.014 | 0.000 | 0.000 | 0.000 |
| *Buchloë dactyloides* (Nutt.) Engelm. | Buffalograss | 0.507 | 2.545 | 7.744 | 22.089 |
| *Carex eleocharis* Bailey | Needleleaf sedge | 1.211 | 1.975 | 2.068 | 3.004 |
| *Carex filifolia* Nutt. | Threadleaf sedge | 0.164 | 0.175 | 0.124 | 0.284 |
| *Chenopodium leptophyllum* (Moq.) Wats. | Slimleaf goosefoot | 0.010 | 0.019 | 0.131 | 0.012 |
| *Chrysothamnus nauseosus* (Pall. Ex Pursh.) Britt. | Gray rabbitbrush | 0.072 | 0.132 | 1.875 | 0.576 |
| *Cirsium undulatum* (Nutt.) Spreng. | Wavyleaf thistle | 0.003 | 0.000 | 0.000 | 0.220 |
| *Conyza canadensis* (L.) Cronq. | Horseweed | 0.286 | 0.016 | 0.000 | 0.000 |
| *Corispermum villosum* Rydb. | Villous bugweed | 0.114 | 0.072 | 0.112 | 0.000 |
| *Cryptantha minima* Rydb. | Miner's candle | 0.000 | 0.009 | 0.000 | 0.000 |
| *Echinocereus viridiflorus* Engelm. | Green-flowered barrel cactus | 0.056 | 0.000 | 0.000 | 0.039 |
| *Elymus elymoides* (Raf.) Swezey | Bottlebrush squirreltail | 1.151 | 0.567 | 0.453 | 0.733 |
| *Eriogonum microthecum* Nutt. | Spreading wildbuckwheat | 0.434 | 1.854 | 0.958 | 0.549 |
| *Eustoma grandiflorum* (Raf.) Shinners | Prairiegentian | 0.010 | 0.000 | 0.016 | 0.000 |
| *Evolvulus nuttallianus* Schult. | Nuttall evolvulus | 0.000 | 0.109 | 0.089 | 0.022 |
| *Gaura coccinea* Nutt. ex Pursh. | Scarlet gaura | 0.008 | 0.031 | 0.050 | 0.042 |
| *Gutierrezia sarothrae* (Pursh.) Britt. & Rusby | Broom snakeweed | 0.717 | 1.628 | 0.797 | 0.132 |

*Table A1.* continued

| Scientific name | Common name | Grazing intensity | | | |
|---|---|---|---|---|---|
| | | Zero | Light | Moderate | Heavy |
| *Haplopappus spinulosus* (Pursh.) DC | Ironplant goldenweed | 0.122 | 0.000 | 0.087 | 0.416 |
| *Heterotheca villosa* (Pursh.) Shinners | Hairy goldenaster | 0.009 | 0.158 | 0.350 | 0.098 |
| *Ipomopsis laxiflora* (Pursh.) Grant | Scarlet gilia | 0.014 | 0.000 | 0.019 | 0.048 |
| *Kochia scoparia* (L.) Schrad. | Fireweed summercypress | 0.000 | 0.000 | 0.070 | 0.000 |
| *Lappula redowski* (Hornem.) Greene | Bluebur stickseed | 0.000 | 0.000 | 0.000 | 0.035 |
| *Lepidium densiflorum* Schrad. | Plains pepperweed | 0.243 | 0.933 | 0.807 | 0.958 |
| *Lesquerella montana* (Gray) Wats. | Mountain bladderpod | 0.005 | 0.000 | 0.009 | 0.000 |
| *Liatris punctata* Hook. | Dotted gayfeather | 0.000 | 0.036 | 0.005 | 0.000 |
| *Lygodesmia juncea* (Pursh.) D. Don | Rush skeletonplant | 0.043 | 0.008 | 0.151 | 0.115 |
| *Machaeranthera tanacetifolia* (H.B.K.) Nees | Tansyleaf aster | 0.014 | 0.000 | 0.000 | 0.022 |
| *Mirabilis lanceolata* (Rydb.) Standl. | Narrowleaf fouroclock | 0.008 | 0.076 | 0.011 | 0.060 |
| *Muhlenbergia torreyi* (Kunth) Hitchc. ex Bush | Ringmuhly | 0.061 | 0.269 | 0.276 | 0.000 |
| *Oenothera coronopifolia* T. & G. | Combleaf evening primrose | 0.125 | 0.008 | 0.700 | 0.110 |
| *Opuntia polyacantha* Haw. | Plains pricklypear | 48.381 | 18.041 | 15.547 | 22.476 |
| *Orobanche fasciculata* Nutt. | Purple broomrape | 0.030 | 0.009 | 0.000 | 0.000 |
| *Osmorhiza obtusa* (Coult. & Ross) Fern. | Sweetroot | 0.000 | 0.029 | 0.039 | 0.000 |
| *Oxytropis sericea* Nutt. | Silky locoweed | 0.000 | 0.000 | 0.000 | 0.084 |
| *Pascopyrum smithii* (Rydb.) A. Love | Western wheatgrass | 4.292 | 0.833 | 2.660 | 0.791 |
| *Penstemon albidus* Nutt. | White penstemon | 0.000 | 0.000 | 0.075 | 0.029 |
| *Penstemon angustifolius* Nutt. ex Pursh. | Narrowleaf penstemon | 0.000 | 0.000 | 0.006 | 0.095 |
| *Picradeniopsis oppositifolia* (Nutt.) Rydb. ex Britt. | Plains bahia | 0.025 | 0.005 | 0.218 | 0.007 |
| *Plantago purshii* R. & S. | Wolly plantain | 0.079 | 0.199 | 0.466 | 0.605 |
| *Psoralea tenuiflora* Pursh. | Slimflower scurfpea | 0.118 | 0.000 | 0.019 | 0.058 |
| *Ratibida columnifera* (Nutt.) Woot. & Standl. | Upright prairie coneflower | 0.000 | 0.000 | 0.000 | 0.291 |
| *Salsola iberica* Sennen & Pau | Russian thistle | 0.030 | 0.000 | 0.009 | 0.012 |
| *Scutellaria brittonii* Porter | Britton's skullcap | 0.121 | 0.000 | 0.066 | 0.000 |
| *Schedonnardus paniculatus* (Nutt.) Trel. | Common tumblegrass | 0.000 | 0.000 | 0.016 | 0.057 |
| *Senecio triangularis* Hook. | Arrowleaf groundsel | 0.045 | 0.000 | 0.028 | 0.113 |
| *Sisymbrium altissimum* L. | Tumbling hedgemustard | 0.034 | 0.000 | 0.093 | 0.000 |
| *Solanum triflorum* Nutt. | Cutleaf nightshade | 0.007 | 0.000 | 0.000 | 0.000 |
| *Sophora nuttalliana* Turner | Silky sophora | 0.055 | 0.000 | 0.060 | 0.000 |
| *Sphaeralcea coccinea* (Nutt.) Rydb. | Scarlet globemallow | 1.272 | 0.886 | 1.332 | 1.398 |
| *Sporobolus cryptandrus* (Torr.) Gray | Sand dropseed | 0.686 | 2.768 | 0.734 | 1.443 |
| *Stipa comata* Trin. & Rupr. | Needle-and-thread | 7.265 | 1.998 | 0.026 | 0.127 |
| *Tagetes patula* L. | Wild marigold | 0.000 | 0.000 | 0.000 | 0.007 |
| *Thelesperma filifolium* (Hook.) Gray | Greenthread | 0.000 | 0.104 | 0.043 | 0.000 |
| *Townsendia grandiflora* Nutt. | Bigflower townsendia | 0.002 | 0.000 | 0.000 | 0.077 |
| *Tradescantia occidentalis* (Britt.) Smyth | Prairie spiderwort | 0.097 | 0.000 | 0.000 | 0.000 |
| *Vulpia octoflora* (Walt.) Rydb. | Common sixweeksgrass | 0.015 | 0.039 | 0.096 | 0.424 |

## References


Anderson V.J. and Briske D.D. 1995. Herbivore-induced species replacement in grasslands: Is it driven by herbivory tolerance or avoidance? Ecol. Appl. 5: 1014–1024.

Archer S., Garrett M.G. and Detling J.K. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72: 159–166.

Biondini M.E., Patton B.D. and Nyren P.E. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecol. Appl. 8: 469–479.

Brown J.H. and Heske E.J. 1990. Control of a desert-grassland transition by a keystone rodent guild. Science 250: 1705–1707.

Collins S.L. 1987. Interaction of disturbances in tallgrass prairie: A field experiment. Ecol. 68: 1243–1250.

Collins S.L., Knapp A.K., Briggs J.M., Blair J.M. and Steinauer E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280: 745–747.

Duncan P. and Jarman P.J. 1993. Conservation of biodiversity in managed rangelands, with special emphasis on the ecological effects of large grazing ungulates, domestic and wild. In: Baker M.J. (ed.), Grasslands for Our World. SIR Publishing, Wellington, pp. 776–783.

England R.E. and DeVos A. 1969. Influence of animals on pristine conditions on the Canadian grasslands. J. Range Manage. 22: 87–94.

Fisser H.G., Lester J.E., Mitchell G.C. and Bledsoe L.J. 1969. Preliminary report of methodology and results for analyses of plant pattern project research on the Pawnee Site. US IBP Grassland Biome Tech. Rep. 9.

Fuhlendorf S.D. and Smeins F.E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. J. Veg. Sci. 8: 819–828.

Guo Q. and Rundel P.W. 1997. Measuring dominance and diversity in ecological communities: choosing the right variables. J. Veg. Sci. 8: 405–408.

Hansen R.M. and Gold I.K. 1977. Blacktail prairie dogs, desert cottontails, and cattle trophic relations on shortgrass range. J. Range Manage. 30: 210–214.

Hart R.H. and Ashby M.M. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. J. Range Manage. 51: 392–398.

Hart R.H. and Hart J.A. 1997. Rangelands of the Great Plains before European settlement. Rangelands 19: 4–11.

Hartnett D.C., Hickman K.R. and Fischer Walter L.E. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J. Range Manage. 49: 413–420.

Heltshe J.F. and Forrester N.E. 1983. Estimating species richness using the jackknife procedure. Biometrics 39: 1–11.

Hobbs N.T., Schimel D.S., Owensby C.E. and Ojima D.S. 1991. Fire and grazing in the tallgrass prairie: Contingent effects on nitrogen budgets. Ecol. 72: 1374–1382.

Hobbs R.J. and Huenneke L.F. 1992. Disturbance, diversity, and invasion: Implications for conservation. Cons. Biol. 6: 324–337.

Jefferies R.L., Klein D.R. and Shaver G.R. 1994. Vertebrate herbivores and northern plant communities: Reciprocal influences and responses. Oikos 71: 193–206.

Johnson H.B. and Mayeux H.S. 1992. A view of species additions and deletions and the balance of nature. J. Range Manage. 45: 322–333.

Kautz J.E. and Van Dyne G.M. 1978. Comparative analyses of diets of bison, cattle, sheep, and pronghorn antelope on shortgrass prairie in northeastern Colorado, U.S.A. In: Hyder D.N. (ed.), Proc. 1st Rangeland Congr. Soc. Range Management., Denver, CO, pp. 438–443.

Klipple G.E. and Costello D.F. 1960. Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the Central Great Plains. In: US Dept. Agric. Tech. Bull. 1216. US Govt. Print. Office, Washington DC US Dept. Agric. Tech. Bull. 1216. US Govt. Print. Office, Washington DC.

Larson F. 1940. The role of bison in maintaining the short grass plains. Ecol. 21: 113–121.

Lauver C.L. 1997. Mapping species diversity patterns in the Kansas shortgrass region by integrating remote sensing and vegetation analysis. J. Veg. Sci. 8: 387–394.

Lester J.E. and Fisser H.G. 1970. *Opuntia* clump size variation on the shortgrass plains, Pawnee Site, Nunn, Colorado. J. Colo.-Wyo. Acad. Sci. 7: 37–38.

Magurran A.E. 1988. Ecological Diversity and Its Measurement. Princeton Univ. Press, Princeton, New Jersey.

McNaughton S.J. 1994. In: Schulze E.-D. and Mooney H.A. (eds), Biodiversity and Ecosystem Function. Springer-Verlag, Berlin, pp. 361–383.

McNaughton S.J., Banykiwa F.F. and McNaughton M.M. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278: 1798–1800.

Milchunas D.G., Lauenroth W.K. and Chapman P.L. 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. Oecologia 92: 520–531.

Milchunas D.G., Lauenroth W.K., Chapman P.L. and Kazempour M.K. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. J. Veg. Sci. 1: 375–384.

Milchunas D.G., Sala O.A. and Lauenroth W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. Amer. Natur. 132: 87–106.

Paine R.T. 1966. Food web complexity and species diversity. Amer. Natur. 100: 65–75.

Pielou E.C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theoret. Biol. 10: 370–383.

Plumb G.E. and Dodd J.L. 1993. Foraging ecology of bison and cattle on a mixed prairie: Implications for natural area management. Ecol. Appl. 3: 631–643.

Risser P.G. 1971. Plant community structure. In: French N.R. (ed.), The Grassland Biome: Analysis and Synthesis of First Year Data. Range Sci. Dept. Sci. Ser. 10. Colorado State University, Fort Collins, CO, pp. 41–58.

Risser P.G., Birney E.C., Blocker H.D., May S.W., Parton W.J. and Wiens J.A. 1981. The True Prairie Ecosystem. Hutchinson Ross, Stroudsburg, Pennsylvania.

Schuman G.E., Reeder J.D., Manley J.T., Hart R.H. and Manley W.A. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. J. Ecol. Appl. 9: 65–71.

Schwartz C.C. and Ellis J.E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18: 343–353.

Shannon C.E. and Weaver W. 1949. The Mathematical Theory of Communication. Univ. Illinois Press, Urbana, IL.

Shoop M.S. and McIlvain E.H. 1963. The micro-unit forage inventory method. J. Range Manage. 16: 172–179.

Simpson E.H. 1949. Measurement of diversity. Nature 163: 688.

Singh J.S., Bourgeron P. and Lauenroth W.K. 1996. Plant species richness and species-area relations in a shortgrass steppe in Colorado. J. Veg. Sci. 7: 645–650.

Tilman D., Lehman C.L. and Thomson K.T. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proc. Natl. Acad. Sci. 94: 1857–1861.

Vavra M., Rice R.W., Hansen R.M. and Sims P.L. 1977. Food habits of cattle on shortgrass range in northeastern Colorado. J. Range Manage. 30: 261–263.

Weltzin J.F., Archer S. and Heitschmidt R.K. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. Ecol. 78: 751–763.

West N.E. and Whitford W.G. 1995. The intersection of ecosystem and biodiversity concerns in the management of rangelands. In: West N.E. (ed.), Biodiversity on Rangelands. Utah State University, Logan, UT, pp. 72–79.

Whittaker R.H. 1965. Dominance and diversity in land plant communities. Science 147: 250–260.

Woodward F.I. 1994. How many species are required for a functional ecosystem? In: Schulze E.-D. and Mooney H.A. (eds), Biodiversity and Ecosystem Function. Springer-Verlag, Berlin, pp. 271–291.

Wright H.A. and Bailey A.W. 1980. Fire ecology and prescribed burning in the Great Plains–a research review. In: USDA Forest Serv. Gen. Tech. Rep. INT-77. USDA Forest Serv. Gen. Tech. Rep. INT-77.