



Grazing effects on aboveground primary production and root biomass of early-seral, mid-seral, and undisturbed semiarid grassland

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ABSTRACT

Annual/perennial and tall/short plant species differentially dominate early to late successional shortgrass steppe communities. Plant species can have different ratios of above-/below-ground biomass distributions and this can be modified by precipitation and grazing. We compared grazing effects on aboveground production and root biomass in early- and mid-seral fields and undisturbed shortgrass steppe. Production averaged across four years and grazed and ungrazed treatments were 246, 134, and 102 g m⁻² yr⁻¹ for the early-, mid-seral, and native sites, respectively, while root biomass averaged 358, 560, and 981 g m⁻², respectively. Early- and mid-seral communities provided complimentary forage supplies but at the cost of root biomass. Grazing increased, decreased, or had no effect on aboveground production in early-, mid-seral, and native communities, and had no effect on roots in any. Grazing had some negative effects on early spring forage species, but not in the annual dominated early-seral community. Dominant species increased with grazing in native communities with a long evolutionary history of grazing by large herbivores, but had no effects on the same species in mid-seral communities. Effects of grazing in native communities in a region cannot necessarily be used to predict effects at other seral stages.

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1. Introduction

The amount and timing of aboveground net primary production (ANPP) of different seral communities can differ because they may be composed of species that allocate growth differently above-versus below-ground. ANPP may also differ among communities because they emerge and grow at different times in relation to timing of seasonal precipitation in different years. Further, ANPP may differ among communities due to successional developmental stage (Odum, 1969). Grazing has a wide range of effects on ANPP of communities across the world (Milchunas and Lauenroth, 1993). The effects of grazing across stages of secondary succession within a region have been little studied, but one study in the United Kingdom observed that effects can be greater in early stages of secondary succession than mid (Gibson et al., 1987 and citations).

Large areas previously planted to row-crops in the western US have been seeded to grassland under the Conservation Reserve Program (CRP) and are interspersed among native undisturbed

communities. Many contracts under the program are nearing termination (Barbarika et al., 2005) and those lands will be grazed, reverted to row-crop agriculture, or re-enrolled. Information on the capacity for these seeded grasslands to withstand grazing pressure is limited because grazing was not historically a management option for CRP, although it may now be allowed based on local resource and invasive species conditions. There are a few studies of secondary succession in either singly grazed (summarized in Peters et al., 2008) or singly ungrazed (Munson and Lauenroth, 2011) shortgrass steppe, but the only studies we are aware of that assess livestock grazing effects are on 14 years of succession in native pastures where white-grub outbreaks produced small-scale patch disturbances by consuming grass roots (Coffin et al., 1998) and a study of the post-year effects of a single-year emergency grazing (Cade et al., 2005). These studies found very small or no effects of grazing, respectively.

Both succession models (reviewed in Peters et al., 2008) and state and transition models (Natural Resource Conservation Service, 2002) for the *Bouteloua/Buchloe* community in shortgrass steppe recognize an initial stage dominated by annual opportunistic, invasive species after cropland has been abandoned. Communities never plowed or subjected to large-scale disturbances other than those such as fire that occurred prior to

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European human settlement are dominated by the grasses *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffith (blue grama), *Buchloe dactyloides* (Nutt.) J.T. Columbus (buffalo grass), and the cactus *Opuntia polyacantha* Haw. (plains pricklypear), the dominant forb *Sphaeralcea coccinea* [Nutt.] Rydb. (scarlet globemallow) and very few annual and/or exotic species (Milchunas et al., 2008), and both successional and state-and-transition models agree here as well. Succession to a community with a large component of the above species can take variable but long periods of time based on recent studies of cropland abandoned during the severe “dust-bowl” drought of the 1930’s (Coffin et al., 1996) or ungrazed CRP fields planted up to 20 years prior to study (Munson and Lauenroth, 2011). Mid-seral communities can have variable compositions (Peters et al., 2008) but are not dominated by annuals like early seral communities and are not dominated by the above core shortgrass steppe species. We established grazed and ungrazed treatments on a newly planted CRP field dominated by annuals, a mid-seral 16–20 year-old CRP field lacking or having very few *B. dactyloides*, *O. polyacantha*, and *S. coccinea*, and with only a small portion of the *B. gracilis* cover of never-plowed communities.

The semi-arid shortgrass steppe is a plant community that has co-evolved with intense grazing by large herds of native bison for 10,000 years and is particularly tolerant to grazing by livestock (Milchunas et al., 2008). A second important selection pressure on development of the plant community is the low 340 mm yr⁻¹ of precipitation and frequent severe droughts. The convergent (complimentary) selection pressures of aridity (competition for belowground resources) and grazing by generalist herbivores (avoidance of herbivory) have produced a plant community where 90% of plant biomass is belowground (Milchunas and Lauenroth, 2001; Milchunas et al., 1988), similar to that observed in Inner Mongolian grasslands (Gao et al., 2008). Heavy grazing results in horizontal spread of the dominant shortgrasses and a “grazing lawn” structure (McNaughton, 1984; Milchunas and Lauenroth, 1989) whereby annual, invasive, and exotic species are found in low abundance compared with ungrazed native communities (Milchunas et al., 1992). This is often opposite to newly seeded grasslands in this region where invasive species can be abundant in plant-interspaces in the recently plowed/disked soils (Baer et al., 2009; Munson and Lauenroth, 2011). Mid-seral CRP sites in the shortgrass steppe region are often dominated by tall rather than shortgrass species due to the seed mix planted during early years of the program where soil stabilization was the dominant objective, seed of native grass species were unavailable in sufficient quantity, and exotic grass species were often sown (Baer et al., 2009; Cade et al., 2005).

The different characteristics of species among early-seral, mid-seral, and native shortgrass steppe have implications for the way communities may differ in aboveground versus belowground plant biomass and the ways that grazing may affect that biomass. The ratio of belowground biomass to aboveground biomass allocation is generally greater in perennials than annuals (Jackson and Roy, 1986; Ploschuk et al., 2005; Schenk and Jackson, 2002) and in short than tall species (Yonghua et al., 2008). Tall grasses are generally more susceptible to decline with grazing (Díaz et al., 2007; Milchunas et al., 1988). Perennial exotic grass species in tall grass prairie that were selected for forage production allocate more biomass aboveground than belowground compared with native perennial grass species (Wilsey and Polley, 2006).

These above- and below-ground structural differences may in turn affect other system characteristics. Some researchers have concluded that grasses established under the CRP in the shortgrass steppe region have contributed to a decline in habitat availability and quality for endemic wildlife due to excessive height of

vegetation and fragmentation of shortgrass dominated landscapes (Samson et al., 2004). Differences in root versus shoot inputs of carbon to soils can affect carbon sequestration (Christian and Wilson, 1999; Munson, 2009) as well as forage availability to herbivores and habitat structure for wildlife. A unit of root compared to shoot biomass contributes more to soil-C sequestration (Rasse et al., 2005) and root production is much greater than shoot production in native shortgrass steppe (Milchunas and Lauenroth, 2001).

The broad objective of this study was to assess aboveground production and root biomass of early-seral and mid-seral CRP fields compared to native shortgrass steppe in grazed and ungrazed treatments to better understand ecological effects of grazing on succession as well as to help guide future land-use options for management. Heavy grazing of native shortgrass steppe has small but negative effects on ANPP (Milchunas et al., 1994) and root biomass (Milchunas and Lauenroth, 1989) but may have different effects on transitioning communities. Grazing maintains native community dominants but decreases in cool-season species are limiting for livestock and wildlife coming out of winter in this warm-season dominated community (Milchunas et al., 2008). Our hypotheses were that:

- Irrespective of grazing treatment, community order with respect to ANPP will be early-seral > mid-seral > native shortgrass steppe and in terms of root biomass would be the inverse order.
- Grazing effects decrease ANPP more in early- and mid-seral communities than in native shortgrass steppe (based on the greater abundances in the former of tall annual forb and tall grass species more susceptible to decline with grazing and more likely to allocate more aboveground).
- Grazing effects increase root biomass more in early- and mid-seral communities than in native shortgrass steppe (due to shifts toward relatively greater belowground allocation by grazing selected dominant perennial shortgrasses).
- Grazing moves seral communities toward the native community structure through increases in native community dominants, and decreases herbivore-limited early-emerging cool-season species in all communities.

2. Methods

2.1. Study sites

The CRP study sites were established in north-central Colorado, U.S.A., near Briggsdale and native undisturbed shortgrass steppe grassland sites were located at the Central Plains Experimental Range (CPER) (lat. 40E 49' N, long. 104E 46' W). Long-term (59 yr) mean annual precipitation recorded at the Briggsdale weather station was 331 mm yr⁻¹ (standard deviation = 92 mm yr⁻¹) with 71% of the precipitation occurring during the May through September growing seasons, and 340 mm for the CPER for the same years. Precipitation during the study period is presented in the discussion section. All sites are level uplands topographically, with soils a mix of fine-loam and fine or coarse sandy loam.

The seeded CRP grasslands were a newly planted 130 ha field adjacent to a 79 ha mid-seral field planted in 1989. Both fields were previously in a long-term winter wheat/fallow system. The mid-seral field had been planted with a mix of *B. gracilis* (50%) a native shortgrass, *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama) (25%) a native but not to these sites, and *Bromus inermis* Leyss. (smooth brome) (25%) an exotic perennial grass from Eurasia. The early-seral CRP field was planted in 2003 to a seed

mixture comprised of *Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass) (30%), *B. gracilis* (20%), *B. curtipendula* (20%), *Nassella viridula* [Trin.] Barkworth (green needle grass) (10%), *Panicum virgatum* L. (switchgrass) (10%), and *Dalea purpurea* Vent. (purple prairie clover) (10%). Previous to seeding the CRP mix the early-seral field was planted to alternating strips of wheat and forage sorghum as cover crops. The undisturbed native sites are dominated by *B. gracilis*, *B. dactyloides*, *O. polyacantha*, the dominant forb *S. coccinea*, and the dominant sub-shrub *Artemisia frigida* Willd. (prairie sagewort).

The early- and mid-seral fields were divided into grazed and ungrazed treatments and six replicate plots (10 m by 20 m) were randomly located in each field-age and grazing treatment. The early-seral field grazing treatment plots were further stratified by strips previously planted to wheat (three plots) or sorghum (three plots) cover crops the year prior to seeding (see Milchunas et al. (2011) for details on the cover-crops). Plots were not grazed until three years after planting. Exclosures (100 m by 100 m) were constructed in each of six undisturbed native pastures (each 130 ha) in 1991. Both native and seral sampling plots were on similar level-upland topography. To mitigate pseudo-replication issues at the CRP fields, pre-grazing-treatment data were collected whereby any problem due to a single pasture nature would be detected, and all three seral-age sites spanned several soil-types as defined by Natural Resource Conservation Service soil maps, so no field represented one single condition, but grazing treatments were paired across the fence.

Grazing treatments in the seeded grasslands were applied opportunistically based on different objectives for the early- and mid-seral fields. Objectives in the early-seral field were to flash graze early in the spring to set back the canopy development of dominant annual forbs and grasses such as *Kochia scoparia* [L.] (Schrud) (burningbush), *Salsola iberica* [Sennen & Pau] Botsch. ex Czerep. (Russia thistle), *Sisymbrium altissimum* L. (tall tumbledustard), and *Bromus tectorum* L. (cheatgrass) prior to availability of *P. smithii* and then again later in the growing season after boot stage. Objectives in the mid-seral field were to graze exotic cool-season *B. inermis* before the planted native warm-season grasses had fully emerged, and then again late-season when the growth of this species had slowed. Thus, both CRP fields were grazed for intense, short periods using from 31 to 35 cow-calf-pairs over one to two days in the early-seral field and two to three days in the mid-seral field in each of two grazing periods (early: April–May, and late: Aug.–Oct.). We term these grazing treatments “moderate-to-heavy” because heavy grazing occurred in the later periods during two years in what otherwise was considered moderate stocking. Objectives in the undisturbed native pastures were to maintain growing-season-long moderate intensity grazing initiated in 1939. Grazing of the native shortgrass steppe pastures begins in late May, approximately one month after the start of the cool-season growth period, and extends for a maximum of 184 days (late November). The length of the grazing period depends upon the time necessary to achieve the intensity criteria of 33.6 g m⁻² residual standing plant biomass at the end of the growing season, which is 40% utilization if averaged over years (Milchunas et al., 2008). These native pastures and exclosures were used as a comparison of the predominant management practices in the region in recent time for native shortgrass steppe with the opportunistically managed seeded grasslands. We realize the ungrazed native treatments were in place longer than the ungrazed seeded grasslands, but consider these ungrazed sites a representation of the longer-term stable ungrazed condition (see Milchunas (2011) for comparisons of the 1991 exclosures used in this paper and those established in 1939 in terms of convergence for the dominant *B. gracilis*).

2.2. Vegetation sampling

Grazing treatments achieved at sampling locations were estimated annually as differences between paired caged versus uncaged plant biomass (utilization, removal) because stocking rates varied annually depending on precipitation effects on primary production and because grazing intensities vary with location within any large, moderately grazed pasture. At each plot in the CRP fields, two movable cages (1.23 m², made from large 15 cm mesh concrete reinforcing wire) to prevent grazing by cattle were relocated randomly each spring to prevent overwinter snow capture effects. Total plant utilization was estimated by visually comparing the difference in vegetation biomass inside each cage to adjacent biomass outside the cage at the end of the grazing and plant growth season. While a qualitative estimate, visual estimates have been historically compared to a subsample of quantitatively clipped residual forage in CPER pastures as a quality control practice for visually derived estimates (Flombaum and Sala, 2007; Hart et al., 1995).

After visual estimates of grazing intensity were obtained from caged versus uncaged biomass, ANPP was estimated by clipping total recent-dead-plus-live vegetation inside the movable cages (not including previous year's dead material) at a height just above grass-crown level in early autumn at peak-standing crop of current-year growth. This method gives a better estimate of ANPP compared with summation of positive increments thru a growing season based on comparisons with the ¹⁴C labeling method (Milchunas and Lauenroth, 1992), and also provides a means of directly comparing aboveground and root biomass since both can also be considered a standing biomass estimate. Quadrats differed between CRP and native sites because of the very different clumped versus lawn-like spatial distribution of biomass in CRP and native grasslands, respectively. Quadrats in CRP fields were 0.3 m² (100 cm × 30 cm) with 12 in each treatment-field type (48 total quadrats yr⁻¹). Clipping in the native grassland was in five 0.25 m² quadrats in each treatment in each replicate (60 total quadrats yr⁻¹). ANPP was sampled at all locations in 2005 and 2007 through 2009, with the 2005 serving as a pre-grazing-treatment sample year. Samples were oven-dried at 55 °C (for at least two weeks in a forced-air oven, which is much longer than the time necessary to reach a constant weight) and weighed.

Roots were cored at two locations in each replicate in each grazing treatment in each grassland type (72 cores yr⁻¹) using a 66.5 mm inside-bit-diameter core driven to a depth of 40 cm. Roots were sampled in a pre-grazing-treatment year (2005) and after five years of grazing treatment (2011) at all CRP sites, but only in 2011 at native shortgrass steppe sites. Roots were separated from soil using a flotation method and captured on a 0.5 mm sieve (Milchunas, 2012), oven-dried at 55 °C for two weeks, weighed, ashed in a muffle furnace at 600 °C and weighed for soil contamination correction to an organic matter basis.

Basal cover was sampled 2005–2009, with 2005 and 2006 serving as pre-grazing-treatment sample years at the CRP sites. Basal cover by species, litter, and bare ground were estimated visually using 20 Daubenmire quadrats (0.1 m²) randomly located in each replicate of each treatment. These data were used to describe the composition of the vegetation in terms of two groups of species, spring forage and dominants of native undisturbed shortgrass steppe. Species emerging early and providing forage after winter are a limiting factor for livestock and wildlife in this predominantly warm-season dominated plant community, and the dominant matrix species of native communities is used to contrast the abundant early-season emerging annuals on the CRP fields with the abundant producers later in the season in native communities. Two years of pre-treatment data were collected for basal cover in early- and mid-seral communities.

2.3. Statistical analysis

The statistical design is a two-factor repeated measures analyses of variance. Eight fields are analyzed as if the treatment factor had been randomly assigned to the 48 plots. The year effect was treated as a repeated measure with autoregressive, lag one correlation structure on the random errors. A significant treatment by year interaction would indicate that treatment differences depended on year; therefore, follow-up comparisons of treatments were done separately by year. *A-priori* treatment contrasts for grazing effect and the grazing by age interaction were tested within each year. Three replicates in the newly planted CRP field were previously planted to wheat and three were previously planted to sorghum cover crops prior to seeding the CRP grassland species. The two cover crop types had large effects on native grass establishment and invasive species composition in the early-seral community and these effects were previously reported in Milchunas et al. (2011). In these analyses, cover crop effect in the newly planted field was accommodated using a covariate adjustment, which averaged residuals for the two cover crops. Root biomass data were analyzed as above for CRP sites only for 2005 and 2011, and for all three sites for 2011 separately because root biomass was not collected on native treatments in 2005. Grazing effect comparisons were made by comparing least square means. ANPP data were log transformed and cover data were square-root transformed to meet ANOVA assumptions of equal variances.

3. Results

Precipitation was below the long-term annual average during the year and autumn of seeding (2003) and during the first three growing-season years (2004–2006). These years included periods of drought and severe drought interspersed with periods of average spring or summer precipitation (Fig. 1). The spring and late autumn of 2005 had good precipitation, but July, August, and September were very dry. Below average-precipitation occurred during 2007 but there were no long periods of severe drought. Heavy late August storms in 2008 elevated total annual precipitation well above the long-term mean but most other months were very dry resulting in a prolonged growing-season drought. A wet spring and summer

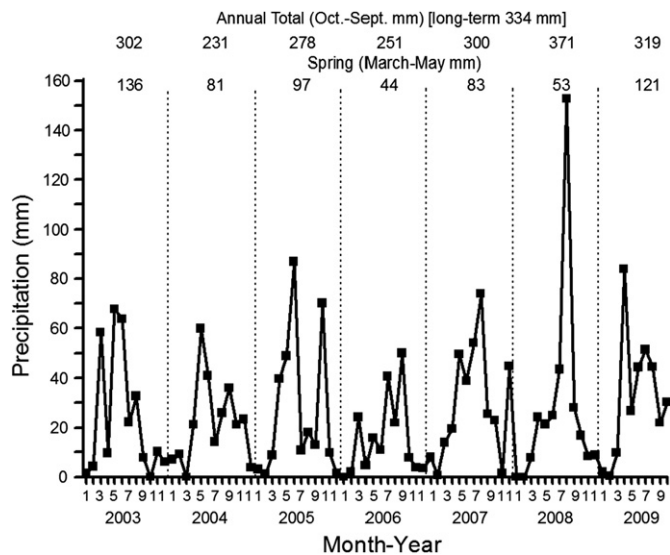


Fig. 1. Monthly, spring cool-season (March–May), and mean annual precipitation (mm, Oct. previous year through Sept. current year) from 2003 to 2009 at the Briggsdale, Colorado weather station approximately 5 km southeast of study area.

growing season occurred in 2009 and the timing of precipitation was well distributed through August, whereby plant greening and leaf-rolling were not observed through much of the rapid growth period. The precipitation pattern in 2009 produced prolific flowering and seeding of all functional groups even though the mean annual precipitation was below average due to a dry previous late autumn and winter.

Estimated levels of consumption in the grazed treatment for 2007 were 59% ± 15 (SD) for the early-seral field, 64% ± 13 (SD) for the mid-seral field, and 52% ± 17 (SD) in native shortgrass steppe. Grazing was deferred in 2008 until late in the year due to early drought conditions precluding a comparable estimation of consumption. Grazing intensities in 2009 were estimated as 40% ± 21 (SD) for the early-seral field, 57% ± 7 (SD) for the mid-seral field, and 41% ± 18 (SD) in native shortgrass steppe.

ANPP generally followed annual and seasonal patterns of exceptionally favorable or unfavorable precipitation (Fig. 2). In 2005, the good early season precipitation resulted in high ANPP for the abundant early-season annual forbs, but the drought mid-season resulted in only average productivity for the native sites. The prolonged drought in 2008 resulted in very low ANPP across all communities and the good timing between rain-events and good seasonal distribution in 2009 resulted in very high ANPP across all communities and particularly the native site. Both extended drought and very good all-season precipitation resulted in relatively more uniform ANPP across seral stages. In contrast, average or seasonally skewed patterns resulted in large differentiation among stages, with high to low ANPP order of early > mid > native seral communities. The early-seral community dominated by annuals had even greater ANPP than mid-seral and native communities during the severe drought year of 2008 but observations indicated this was due to germination and growth of many annual forbs after the heavy rains in August (Fig. 1).

Grazing treatment modified ANPP within communities only in the early- and mid-seral communities and only in some productive years (Fig. 2). In both non-drought years (2007, 2009), the ungrazed treatment in the mid-seral community had greater ANPP than the grazed treatment. In contrast, the grazed early-seral community had greater ANPP than the ungrazed but this occurred only in 2009. Grazing had no effect on ANPP in the grazed native communities in

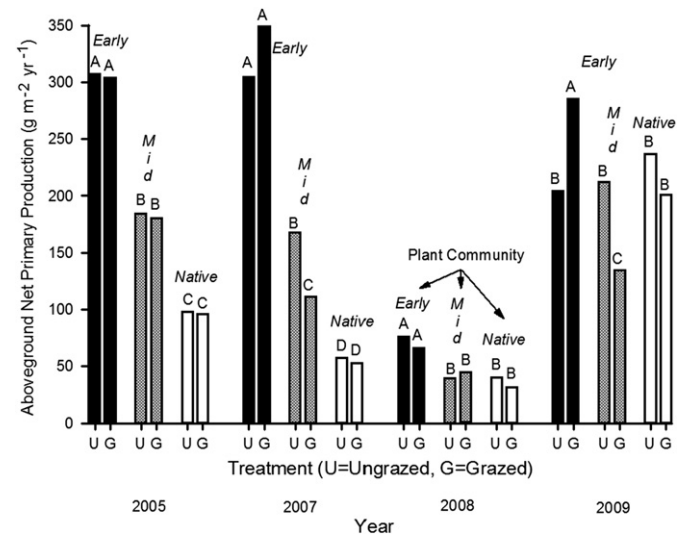


Fig. 2. Aboveground net primary production ($\text{g m}^{-2} \text{yr}^{-1}$) in early-seral and mid-seral seeded grassland and native shortgrass steppe in ungrazed and grazed treatments for four years. The year 2005 for seeded grasslands was pre-grazing-treatment, while all years are for grazing treatments at the native site. Bars within a year not sharing a common letter are significantly different.

any of the four years, although the grazed treatment always tended to be lower than the ungrazed.

We assess here the composition of the plant communities in terms of basal cover of the shortgrass steppe dominants as a measure of degree of recovery to native conditions. Shortgrass steppe dominants were practically absent from the early-seral field, and in the mid-seral community averaged only 12% of that found in native shortgrass steppe communities (Fig. 3). Grazing did not significantly alter the basal cover of shortgrass steppe dominants in the mid-seral community, but increased them significantly in three of five years in the native community. Dissimilarity indices comparing early-seral versus native communities were always greater than 95%, and mid-seral versus native communities ranged from 55 to 80% dissimilarity (data not shown, calculated using Whittaker Index of Community Association).

The basal cover of spring forage availability is also assessed because spring forage is limiting for secondary production in warm-season dominated native communities for animals coming out of winter nutritional stress (Milchunas et al., 2008). Spring forage species did not include all C₃ or cool-season species, but only those providing very early good growth per individual plant. Basal cover of early spring forage species was generally very low in the mid-seral community compared with either the early-seral or native communities (Fig. 4). Early spring forage species in the early-seral communities varied by year relative to native grassland. Its basal cover was equal to, less than, and greater than in the native with the latter occurring in both the drought and good precipitation years. For the 2007, 2008, and 2009 years when grazing treatments were imposed, grazing treatment had no significant effect on basal cover of spring forage species in the early seral communities and decreased this species group in two of three years in the mid-seral. Grazing treatments occurred all years in the native grassland and were significantly greater in three of five years.

Root biomass did not differ between grazing treatments in pre-grazing treatment year (2005) at the early- or mid-seral CRP sites, and did not differ between grazing treatments at early- or mid-seral CRP or at native shortgrass steppe sites in 2011, five years after initiating grazing treatments at the CRP fields and 20 years

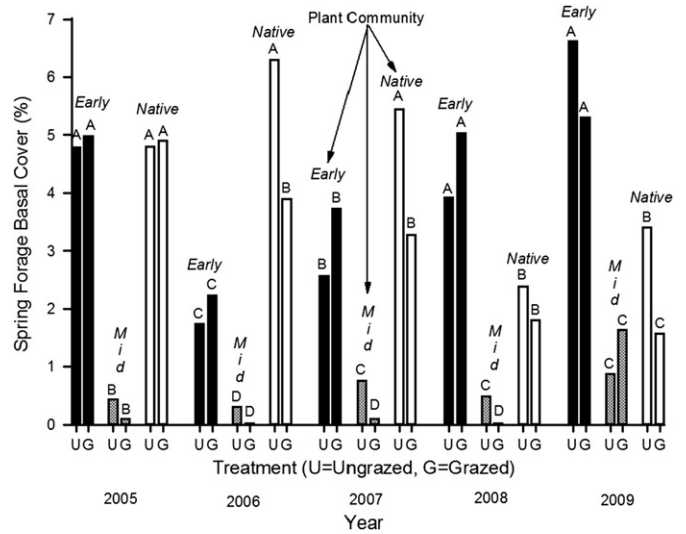


Fig. 4. Basal cover (%) of spring forage species (*Agropyron cristatum* (L.) Gaertn. (crested wheatgrass), *Carex eleocharis* L.H. Bailey (needleleaf sedge), *Kochia scoparia*, *P. smithii*, *Hesperostipa comata* (Trin. & Rup.) Barkworth (needle and thread grass previously *Stipa comata*), and *N. viridula*) in early-seral and mid-seral seeded grassland and native shortgrass steppe in ungrazed and grazed treatments for five years. The years 2005 and 2006 for seeded grasslands were pre-grazing-treatment, while all years are for grazing treatments at the native site. Bars within a year not sharing a common letter are significantly different.

after excluding grazing at the six native shortgrass steppe sites (Fig. 5). Root biomasses among field ages were significantly different, increasing with seral stage. Averages across grazing treatments were 358, 560, and 981 g m⁻² for the early-seral, mid-seral, and native plant communities, respectively.

4. Discussion

Christian and Wilson (1999) found greater shoot mass in fields planted with the tall bunchgrass *Agropyron cristatum* (L.) Gaertn.

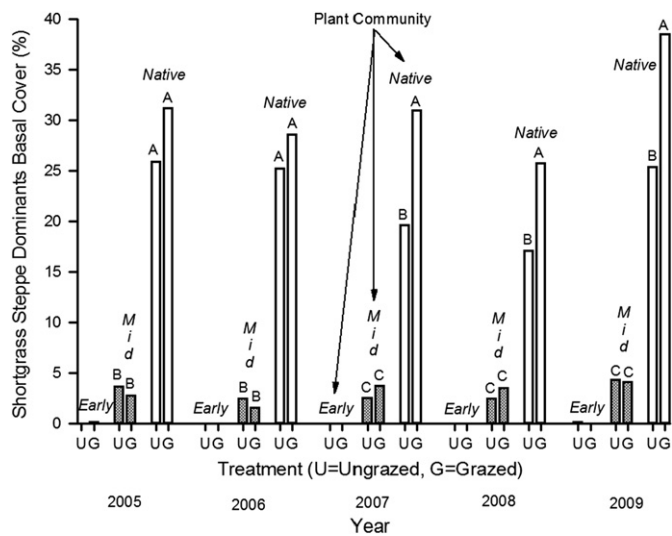


Fig. 3. Basal cover (%) of native shortgrass steppe dominant or matrix species (*B. gracilis*, *B. dactyloides*, *S. coccinea*, and *A. frigida*) in early-seral and mid-seral seeded grassland and native shortgrass steppe in ungrazed and grazed treatments for five years. The years 2005 and 2006 for seeded grasslands were pre-grazing-treatment, while all years are for grazing treatments at the native site. Bars within a year not sharing a common letter are significantly different.

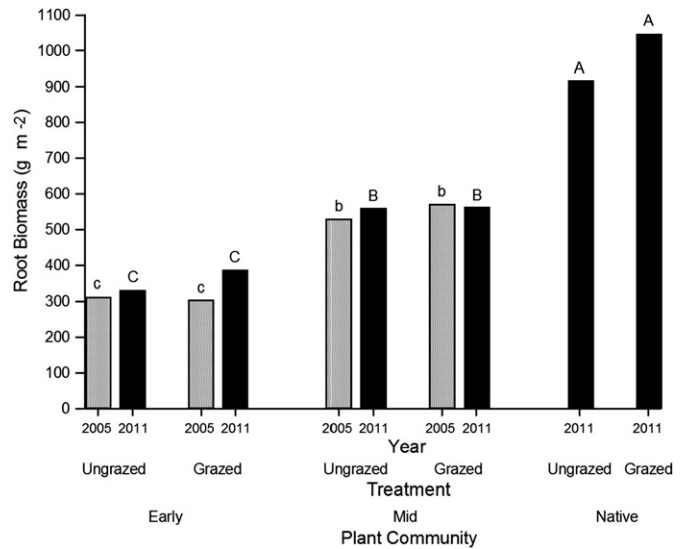


Fig. 5. Root biomass (g m⁻²) to 40 cm depth in early-seral and mid-seral seeded grassland and native shortgrass steppe in ungrazed and grazed treatments in 2005 and 2011. The year 2005 for seeded grasslands was pre-grazing-treatment. Bars within a year not sharing a common letter are significantly different. Bars across year 2011 within a grazing treatment not sharing a common capital letter are significantly different.

(crested wheatgrass) than in successional or native mixed-grass prairie, but much lower root to shoot ratios and lower soil carbon and nitrogen because of the low root mass and lower inputs to soil for the exotic species. In shortgrass steppe, Munson (2009) observed greater aboveground and less belowground primary production in CRP fields than native shortgrass steppe and that soil C and N were correlated with belowground root inputs. Results from this study also indicate that the annual opportunistic forbs dominating early-seral communities can provide large amounts of ANPP at the sacrifice of root biomass. The aboveground biomass of these species can be transient or absent during dry periods but respond with germination and growth after heavy rains occur. A large component of this group, *K. scoparia* is a high-N palatable species, but caution must be used to avoid nitrate poisoning of livestock (Stanton, 2004). The annual forb component of ANPP was also comprised of lesser amounts of *S. iberica* and *S. altissimum* which were not consumed when mature. The mid-seral community provided greater ANPP than native shortgrass steppe in two of four years, which may in part be due to the taller commercial genotype of *B. gracilis* and the relatively tall *B. curtipendula* and *B. inermis* seeded. This tall, conspicuously bunch-grass physiognomy of the mid-seral field also produces distinctly more bare ground interspaces than that observed in the sod-structured native shortgrass steppe, with interspaces only sometimes filled in with rhizomatous *B. inermis*. While belowground net primary production was not estimated, lower root biomasses in both early and mid-seral communities than native shortgrass steppe in this study suggests slow recovery in these fields where establishment of perennial grasses determines rate of recovery in soil organic matter (Burke et al., 1995). The results support our hypothesis that community order with respect to ANPP would be early-seral > mid-seral > native shortgrass steppe and in terms of root biomass would be the inverse order.

Moderate grazing in the native shortgrass steppe community had no significant effect on ANPP in this study. Long-term (1939–1990) data show averages of 75, 71, 68, and 57 g m⁻² yr⁻¹ in ungrazed, lightly, moderately, and heavily grazed native shortgrass steppe, respectively (Milchunas et al., 1994) indicating very little effect of grazing until heavy (~60% of ANPP) levels are reached. Lower intensities of grazing in mid-seral communities such as those studied here may be necessary to avoid reductions in ANPP observed in some years. Grazing of the CRP fields in this study was at greater intensities than desired in 2007 and 2008 because of the difficulty in managing grazing intensity when using relatively large herds in relatively small pastures. Grazing of the annual forb dominated early-seral community had the opposite effect, sometimes increasing ANPP. Many factors could contribute to this, including thinning of old-dead standing residual from previous year, fecal and urine inputs of nitrogen, and hoof-action keeping soil in a more “tilled” state for N-release. The latter two would benefit production of the annual forbs, especially *K. scoparia*, but could potentially be detrimental to native grasses (Blumenthal et al., 2003). Cover of shortgrass steppe dominants were not, however, negatively affected by grazing in this study. The largest component of native shortgrass steppe that occurred in the early-seral community was the rhizomatous perennial grass *P. smithii*, which increased with grazing at this site in some years (Milchunas et al., 2011). *P. smithii* decreases with grazing in all previous studies in native shortgrass steppe (Milchunas et al., 2008) and it is interesting to note the neutral to opposite response in the context of the annual forb dominated community studied here. Hakes and Cronin (2012) also observed greater resistance of a species to grazing in early- compared to late-successional fields and attributed it to associational resistance or avoidance (proximity to neighbor plants influences selection) when their target plant was surrounded by

a greater diversity and abundance of forbs, similar to the difference between the early-seral and native community in this study. Results supported our hypothesis that grazing would have greater negative effects on ANPP in the mid-seral communities with greater abundances of susceptible tall grass species than in native shortgrass steppe, but did not support our hypothesis concerning the early-seral community for susceptibility of the tall annual forbs. Tall annual exotic forbs decrease in abundance when competing with dominant shortgrasses in native communities but ANPP sometimes increased when they dominated the early-seral community and competition was intraspecific.

There were no grazing effects on root biomass in any of the three field stages of succession. Long-term grazing of native shortgrass steppe at moderate intensity since 1939 also has not affected root biomass, although as with ANPP some declines compared with ungrazed treatments have been observed under heavy grazing of lowland swales (Milchunas and Lauenroth, 1989; Milchunas et al., 1998). We reject our hypothesis that grazing would increase root biomass more at the early- and mid-seral fields than at native sites even though annual and tall grass species that are more susceptible to decline with grazing were more abundant in the CRP fields. Grazing treatments at the CRP fields may not have been long enough to sufficiently shift species composition or the species in this semiarid environment are particularly resistant to belowground change regardless of seral stage.

Native shortgrass steppe dominant species were of very low abundance in the early-seral field due to drought restricting planting success, a common phenomenon in arid and semiarid regions (Hardegee et al., 2011). Seeding success was high in 1989 when the mid-seral fields were planted. Even so, the low cover of native shortgrass steppe dominant species in mid-seral compared to native fields is much greater than differences in ANPP between the fields. This may in part be due to the taller genotypes of *B. gracilis* planted, as well as planting of persistent perennial tall grasses that were either non-native (*B. inermis*) or non-native to these particular sites (*B. curtipendula*). Occupancy of space by these seeded species may account for the low immigration of native non-seeded perennial grasses in these fields (Milchunas and Vanderver, 2013) and a slow recovery based on community species similarity indices. Grazing increased shortgrass steppe dominant species in native sites, but we reject our hypothesis that grazing would increase their abundance in mid-seral communities, and there was insufficient establishment in the early-seral community to test the hypothesis.

Early-seral communities dominated by invasive annual forbs can provide a source of early cool season forage in some years, but abundances of invasive annuals were low in the mid-seral fields studied here. Early cool season forage did not include the cool season *B. inermis* that was a significant component of the mid-seral community and would provide some later cool season forage but which decreased with grazing (Milchunas and Vanderver, 2013). Grazing also decreased early cool season species in the mid-seral and native communities but had no effect in the early-seral community. We only partially accept our hypothesis that grazing would decrease cool season species abundance in all community types. Lighter grazing intensities than those used in this study may better provide a source of early season forage in communities not dominated by annual cool season forbs.

There are implications of our findings for managers and producers. Very good timing of rainfall events and seasonal distributions of precipitation and prolonged periods of drought both resulted in relative homogeneity in ANPP among community types, while average years and seasonally skewed distributions in precipitation both resulted in large differences among communities,

with early-seral and to a lesser extent mid-seral field providing greater quantities of ANPP. A large proportion of the ANPP in early-seral communities was from early spring species of annual forbs, providing a complimentary supply for animals coming out of winter nutrient stress. Early visual observations in shortgrass steppe of eastern Colorado suggested that heavy concentrations of livestock may prolong the annual-plant stage (Costello, 1943), but this was not evident under the conditions studied here. Although some of the hypothesized positive effects of grazing were not evident in the early years of grazing these communities, grazing generally had relatively small or neutral effects as in native shortgrass steppe. The relatively greater investment of the CRP communities in aboveground compared to belowground biomass and the differences in how the CRP and native communities respond to timing of precipitation indicates that a mix of these fields in a ranch landscape may provide complimentary sources of seasonal forage. With respect to abandoned plowed fields after the severe drought of the 1930's, Costello (1941) suggested that pastures neither dominated by shortgrasses nor by invasive forbs provide a balanced diet for cattle and a mix of from 10 to 20% forbs and shrubs with grasses produced best animal weight gains. Grazing intensities need to be monitored closely to avoid possible lowering of potential productivities, but these communities do not appear especially sensitive to utilization. These conclusions are generally supported by community species composition studies (Milchunas and Vanover, 2013; Milchunas et al., 2011). Although paired grazed-ungrazed sites sampled at both native and CRP fields spanned several soil types, the CRP fields used in this study represent only two ages and years of conversion from cropland, two of many seeded species combinations, and one grazing management possibility. Therefore, we cannot extrapolate results from this study to all CRP fields, seral stages, or types of grazing management, but the seral gradient did represent an early annual stage, a mid-seral perennial stage, and good condition well-managed moderately-grazed native shortgrass steppe that had never been plowed.

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