



Grazing effects on plant community succession of early- and mid-seral seeded grassland compared to shortgrass steppe

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Conservation Reserve Program (CRP); Herbivory; Invasive (weed) suppression; Opportunistic grazing; Grassland recovery after cultivation; Livestock; Restoration; Revegetation; Secondary succession

Nomenclature

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Abstract

Questions: Grazing may speed or slow secondary succession, and the direction may depend on seral stage and relative tolerance of native perennial grasses compared with annual invasive species. How does grazing affect succession where undisturbed communities have a long evolutionary history of grazing by native herbivores and are tolerant to livestock grazing?

Location: Shortgrass steppe, North American Great Plains, Colorado (40°49'N, 104°46'W), USA.

Methods: Ungrazed and grazed early-seral (4–6 yr) and mid-seral (18–20 yr) seeded fields (Conservation Reserve Program) and traditionally grazed native steppe were compared for effects on plant composition in relation to changes expected from regional succession models.

Results: Recovery towards undisturbed native shortgrass steppe for early- and mid-seral communities, respectively, was 19% and 36% for total vegetation cover, 5% and 21% for planted native species, 10% and 88% for non-planted native perennial grasses, only 0.2% and 13% for short grasses, and overall dissimilarity in community species compositions was 97% and 68%. In general, grazing effects were neutral or most often not significant in all years and/or were small in overall community magnitude. The early-seral community displayed more changes indicative of a slowing of succession with grazing (total vegetative and grass basal cover) rather than reducing invasive species (species targeted by timing of grazing), although drought had limited the establishment of grazing-tolerant short grasses. The mid-seral community showed more changes consistent with advancing successional recovery with grazing (overall community dissimilarity, forbs, planted native perennial grasses, tall grasses and target species). However, non-planted native perennial grasses responded negatively to grazing in the mid-seral community and positively in native shortgrass steppe where outside seed would originate.

Conclusions: Grazing effects on particular functional groups and species were not the same across seral stages, were mixed in terms of speeding or slowing succession, and were generally not large at the community level. Evolutionary history of grazing may serve as a general guide but decisions on whether to graze successional grasslands may best be made after assessing whether tolerant perennial short grass species are significant components. Monitoring may then be necessary to determine species responses in particular community matrixes and effects on subsequent immigration of non-seeded native perennial species.

Introduction

Herbivory may speed or slow plant community succession, and synthesis as to where or when each may occur has

primarily been based on studies of specialist herbivores in woody communities, with only four of 34 cases of large generalist grazers in grasslands and none involving livestock and secondary succession (Davidson 1993). Grazing

and mowing in Europe can be a tool for restoring the diversity of native plant species to seeded grasslands by suppressing competition from canopy dominants (Walker et al. 2004), and the effects can be greater in early stages of secondary succession than in mid-stages (Gibson et al. 1987 and citations therein). In restoration and invasive (weed) species control projects, it has been suggested that grazing and fire may enhance native and reduce invasive species abundance if the desired native and undesired invasive species do not share a common evolutionary history or are functionally different (MacDougall & Turkington 2005; D'Antonio & Chambers 2006; Baer et al. 2009). The shortgrass steppe of the North American Great Plains (spanning 3.4×10^5 km²) is an ecosystem that has evolved with heavy grazing by bison for 10 000 yr (Mack & Thompson 1982). Convergent selection pressures of grazing and aridity have shaped a community that is among the most resistant in the world to change under heavy grazing by large generalists (Milchunas et al. 1988, 2008), but grazing effects on secondary succession have not been studied. The broad objective of this study was to assess the effects of cattle grazing on newly seeded early-seral grassland and mid-seral seeded grassland compared with native shortgrass steppe to assess whether the direction of successional state changes in native grazed vs ungrazed communities occurs with grazing during earlier stages of secondary succession with cropland conversion to grassland.

In arid and semi-arid regions row crop production is often economically marginal, and lands are subject to high rates of erosion. Since 1986, the Conservation Reserve Program (CRP) in the USA provides financial assistance to farmers and ranchers to convert eligible croplands to grassland, with over 140 000 km² under the program (Barbarika et al. 2005). Grazing was allowed as a management option only after 2002 and under restricted conditions. Many contracts are nearing termination and those lands will be grazed, reverted to row-crop agriculture, or re-enrolled. Some have questioned the basis for restricting disturbances such as grazing and fire on CRP or grassland restoration projects, as active management may emulate historical ecosystem drivers (Milchunas et al. 2005; D'Antonio & Chambers 2006; Baer et al. 2009), and information on the capacity for these seeded grasslands to withstand grazing pressure may help guide future land-use options and program policy.

Previous studies indicate native shortgrass steppe plant communities subjected to long-term heavy grazing by domestic livestock respond with increased basal cover of perennial short grass species (Gramineae of low stature and prostrate growth form) and total vegetation. Additionally, exotic and weedy invasive species under grazing decrease compared with ungrazed grassland (Milchunas

et al. 1989, 1992). The most abundant opportunistic weed species that invade newly seeded grassland and other heavily disturbed areas are tall annuals that allocate relatively more growth above-ground and overshadow native short grasses that allocate relatively more growth below-ground, permitting them to better compete for soil water and nutrients (Milchunas & Lauenroth 1995; Peters et al. 2008; Munson et al. 2012; Milchunas 2012). The ratio of below-ground biomass to above-ground biomass allocation is generally higher in perennials than annuals (Jackson & Roy 1986; Schenk & Jackson 2002; Ploschuk et al. 2005), indicating perennial species invest energy in root structures that support sustained perennial growth. Plant biomass in shortgrass steppe dominated by short grasses is 90% below-ground (Milchunas & Lauenroth 2001), and this provides an avoidance of herbivory compared with tall annual invasive species and tall grasses (Milchunas et al. 1988, 2008; Díaz et al. 2007), and a functional mechanism for grazing as a potential tool for advancing succession in this and similar arid ecosystems with a long evolutionary history of grazing. Further, perennial exotic seeded grass species in tall-grass prairie that were selected for above-ground forage production can also allocate more resources to above-ground growth relative to native perennial seeded grass species (Wilsey & Polley 2006). Many CRP fields in the shortgrass steppe region were seeded to introduced perennial grasses for erosion control purposes (Cade et al. 2005; and references in Baer et al. 2009 for other communities), or to tall grass species that are native but not to the site, partly because seeds are more easily harvested commercially and are available. These mid-seral grasslands may have lower abundances of invasive weedy tall annual forbs than early-seral communities but still often have species or structural physiognomies that contrast with adjacent shortgrass steppe. Tall grasses established under the CRP in the shortgrass steppe region may have contributed to a decline in habitat availability and quality for endemic wildlife due to excessive height of vegetation and fragmentation of short grass-dominated landscapes (Kamler et al. 2003; McIntyre 2003; Sampson et al. 2004). Less below-ground carbon inputs in CRP fields planted to tall introduced species compared with native communities have been observed in both mixed-grass prairie (Christian & Wilson 1999) and shortgrass steppe (Munson et al. 2012; D.G. Milchunas and M.W. Vandever, Unpublished data) regions.

While tall plant communities and tall plant species are more susceptible to grazing impacts than short ones (Milchunas et al. 1988; Díaz et al. 2007), the timing of grazing can also be used to modify plant community response, because a species may be more or less tolerant of grazing at different phenological stages, and species susceptibility to grazing can vary with seasonal patterns of emergence and

senescence. Grazer selectivity at the species level is another factor that can determine differential defoliation pressures, and palatability of a species can vary with phenology. Opportunistically timed grazing (Westoby et al. 1989) based on plant phenology and grazer preference may be planned to augment specific impacts on plant community composition and trajectories. There are a few studies of secondary succession in grazed shortgrass steppe following abandonment of cropland after the 'dustbowl drought' of the 1930s (Costello 1944; Judd 1974; Coffin et al. 1996; summarized graphically in Peters et al. 2008), but there are no comparisons of grazing intensities or ungrazed treatments except for a study of the post-drought-year effects of a single-year emergency grazing of otherwise ungrazed fields (Cade et al. 2005).

Specific objectives of this study were to use seasonally timed grazing to target particular species components of newly planted 4-yr-old 'early-seral CRP' and 18-yr-old 'mid-seral CRP' fields and compare grazed and ungrazed treatments in these to typical growing season-long, moderately grazed and ungrazed native shortgrass steppe. The newly planted CRP was dominated by invasive annuals. The mid-seral CRP lacked or had very small cover of the sub-dominant species (*Buchloe dactyloides* [Nutt.] J.T. Columbus (buffalo grass), *Opuntia polyacantha* Haw. (plains prickly pear cactus) and *Sphaeralcea coccinea* [Nutt.] Rydb. (scarlet globemallow) and only a small portion of the dominant species (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths (blue grama) of never-ploughed communities. Target species for reductions in the early-seral CRP were *Bromus tectorum* L. and the tall exotic annual invasives (weeds) *Kochia scoparia* (*Brassia scoparia* (L.) A.J. Scott (kochia or burning bush), *Salsola iberica* (Sennen & Pau) Botsch. ex Czerep. (Russian thistle) and *Sisymbrium altissimum* L. (tall tumble mustard), while attempting to minimize impacts on *Pascopyrum smithii* [Rydb.] A. Löve (western wheatgrass). The primary target reduction in the mid-seral CRP was the exotic perennial relatively tall *Bromus inermis* Leyss. (smooth brome) and an increase in the short dominant species of native shortgrass steppe *B. gracilis*. We sampled both fields for 2 yr prior to imposing grazing, and then for 3 yr with grazing treatments. Three yr is a short time in succession dynamics of semi-arid regions, so our use of the term implies shifts in composition that would indicate faster rates of recovery towards the native plant community structure. Our hypothesis was that, in this region where native species are evolutionarily adapted to grazing, grazed treatments will display relatively more characteristics of late-seral stages than ungrazed treatments; specifically, increases in total vegetative basal cover due to the grazer avoidance, horizontal spreading 'lawn structure' (Milchunas & Lauenroth 1989) of below-ground allocating short grasses vs tall grasses, lower dissimilarity

index of overall community species composition compared with native grazed shortgrass steppe and lower abundances of forbs (particularly invasive weed forbs), and increases in seeded native perennial grasses and colonizing perennial grasses (Peters et al. 2008; Munson & Lauenroth 2012). Both grazed and ungrazed shortgrass steppe have low abundances of annual opportunistic invasive weed species and high abundances of grazing-tolerant perennial grasses, while CRP fields have higher abundances of annual forbs and grasses and exotic perennial grass species (Munson & Lauenroth 2012). Therefore, a second hypothesis was that the responses to grazing would be greater in CRP grasslands than shortgrass steppe and in early-seral than mid-seral CRP fields. Alternatively, CRP communities with high abundance of invasive and exotic forbs and grasses and relatively low abundance of native short grasses may have different responses of those components to grazing than in native shortgrass steppe.

Methods

The study sites consisted of two adjoining CRP fields in north-central Colorado, near Briggsdale, and native undisturbed grassland at the Central Plains Experimental Range (CPER). All sites are level uplands topographically, with soils a mix of loams and sandy loams. Land use in the shortgrass steppe region is 70% natural plant communities used for livestock grazing and the remaining mainly dry-land crops with irrigated cropland near waterways (Lauenroth & Milchunas 1992). Approximately 25% of the area surrounding the study sites was ploughed and abandoned during the drought of the 1930s, and only recently have large areas of highly erodible cropland been converted to grassland. Native undisturbed grassland in this study is virgin, never-ploughed grassland that is similar in composition to pre-settlement conditions when large bison herds occupied the region.

Long-term (59 yr) mean annual precipitation recorded at the Briggsdale weather station was 331 mm·yr⁻¹ (SD = 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 was below the long-term annual average during the year and the autumn of seeding (2003) and during the first three growing season years (2004–2006), which included periods of drought and severe drought (Appendix S1). Near average precipitation conditions occurred during 2007. Heavy August storms in 2008 elevated total annual precipitation well above the long-term mean, but most other months were very dry. A wet spring and summer growing season occurred in 2009, and the timing of precipitation was well distributed through August. This latter year's precipitation

pattern produced very high above-ground primary production, and prolific flowering and seeding of all functional groups were seen even though the mean annual precipitation was below average due to a dry previous late autumn and winter.

In 2004 we identified a newly planted 130-ha CRP field adjacent to a 79-ha mid-seral CRP field planted in 1989 for our evaluation. Both fields were previously in a long-term winter wheat/fallow system. The early-seral CRP field was planted to a seed mixture comprised of *Pascopyrum smithii* (30%), *Bromus gracilis* (20%), *Bouteloua curtipendula* (20%), *Nassella viridula* [Trin.] Barkworth (10%; green needle grass), *Panicum virgatum* L. (10%; switchgrass) and *Dalea purpurea* Vent. (10%; purple prairie clover). Previous to seeding the CRP mix, the early-seral field was planted to alternating strips of wheat and forage sorghum as cover crops. Only *P. smithii* established from seeding of the early-seral CRP, and the site was dominated by annual invasive species during this study. The mid-seral field had been planted to a mix of *B. gracilis* (50%) a native short-grass, *Bouteloua curtipendula* (Michx.) Torr. (25%; sideoats grama), a native but not to these sites, and *B. inermis* (25%), an introduced perennial grass from Eurasia. These species still dominated the sites at the time of study. All native undisturbed sites and those adjacent to the CRP sites were dominated by *B. gracilis*, *O. polyacantha* and *B. dactyloides* and the dominant forb *S. coccinea*, with *P. smithii* common but not abundant.

Six replicate plots (10 m × 20 m) within each of the grazed and ungrazed treatments were randomly located across each of the early- and mid-seral fields, but in the early-seral field three plots were randomly located in each of the previous sorghum and wheat strips in each grazing treatment to control for this variability across the uniformly seeded field (see Milchunas et al. 2011; for details on the cover crops). CRP sites were not grazed until spring 2007 (3 yr after planting) but were sampled for 2 yr prior to grazing to mitigate pseudoreplication. Six mowing treatment plots of the same size were established in the early-seral field adjacent to the ungrazed plots. Mowing is a management option for weed suppression in newly planted fields, but not in later seral fields where weed populations have declined. Six 1-ha exclosures were constructed in each of six undisturbed short-grass steppe pastures (each 130 ha) in 1991 adjacent to exclosures established in 1939 randomly on level uplands.

Grazing treatments in the seeded grasslands were applied opportunistically based on different objectives for the early- and mid-seral fields, with some constraints due to landowner schedule and grazing permit agreements between US Forest Service and the landowner. A central watering tank was located where fields and treatments

converged, and access to sites was regulated by electric fence gates. Objectives in the early-seral field were to flash graze (intense, short period) early in the spring to set back canopy development of dominant annual forbs and grasses such as *K. scoparia*, *S. iberica*, *S. altissimum*, and *B. tectorum* prior to availability of *P. smithii*, and then again later in the growing season after boot stage (grass growth stage when inflorescence is enclosed by sheath of uppermost leaf, evident as swelling prior to heading). 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. Objectives in the undisturbed native pastures were to maintain growing-season-long moderate intensity grazing initiated in 1939 (details below), which is the predominant management practices in the region. We realize the ungrazed native treatments were in place longer than the ungrazed seeded grasslands, but again consider these ungrazed sites to represent 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*).

Caged vs uncaged plant biomass estimates of grazing intensity (utilization, removal) were obtained as the primary indicator of grazing treatments (described below), because stocking rates varied annually depending on weather effects on primary production. In general, stocking in the grazed CRP fields ranged from 31 to 35 cow-calf pairs over 1–2 d in the early-seral field and 2–3 d in the mid-seral field in each of two grazing periods (early: April–May, late: August–October). Early season grazing exceptions occurred in 2008 when the early-seral field was not grazed and the mid-seral field was grazed for only 1 d due to very dry conditions, and in the late period in 2008 and 2009 when grazing in both fields was for 3.5–4.0 d. We term these grazing treatments ‘moderate-to-heavy’ because of the very heavy grazing in these later periods in what was otherwise considered moderate stocking. Grazing of the native shortgrass steppe pastures can be from late May through late November, with the length of the grazing period depending on 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 using from 11–29 cow-calf pairs, which is 40% utilization if averaged over years. Mowing treatments on the early-seral field occurred once per summer by cutting all standing vegetation at a height of ca. 10 cm when *K. scoparia* and *S. iberica* were ca. 20 to 25-cm high. 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 drought

conditions, so estimates of consumption were not made. Grazing intensities in 2009 were estimated as $40 \pm 21\%$ (SD) for the early-seral field, $57 \pm 7\%$ (SD) for the mid-seral field, and $41 \pm 18\%$ (SD) in native shortgrass steppe.

Canopy and basal cover by species and litter and bare ground were estimated visually using 20 Daubenmire quadrats (0.1 m^2) randomly located in each replicate of each treatment, with cover percentages estimated in 1% increments up to 10%, and by 5% increments above 10%. At each plot in the seeded fields, two movable cages (1.23 m^2 , made from large 15-cm mesh concrete reinforcing wire) to prevent grazing by cattle were relocated randomly each spring to prevent 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.

The Whittaker (1952) index of community association was calculated to contrast overall community composition differences among treatments for each replicate. This index sums proportional differences between two contrasted communities, and is independent of differences in total abundances of the species (see Milchunas 2006 for detailed examples of index behaviour). Replicate samples of the two ages of CRP fields were compared to replicate samples of grazed native shortgrass steppe because grazing is the evolutionarily historic condition with the least exotic and invasive species (Milchunas et al. 2008).

Foraging selectivity in early-seral and native shortgrass steppe was approximated using Ivlev's (1961) electivity coefficients, calculated based on bites counted by species in 50-m long by 10-cm wide belt transects, with five transects in each replicate in each treatment in 2007. Values range from +1 for highly selected species to -1 for totally avoided species, using the formula $(\% \text{bites} - \% \text{cover}) / (\% \text{bites} + \% \text{cover})$ where %bites are the bites counted for a particular species as a percentage of total bites, and %cover is the canopy cover of the species as a percentage of the total. These types of selectivity estimates can be crude, and were only used based on broad categories of $>0.33 =$ selected for, <0.33 to >-0.33 selected in proportion to abundance, and <-0.33 selected against.

The statistical design was a two-factor repeated measures ANOVA with eight fields analysed as if the treatment factor had been randomly assigned to the 48 plots without restriction. The year effect was a repeated measure with autoregressive, lag 1 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, the grazing by age interaction and the mowing effect

were tested within each year. For all treatments, 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 (weed) species composition, and these effects were previously reported in Milchunas et al. (2011). In this report, we focus on grazing effects across all three field ages. The cover crop effect in the newly planted field was accommodated using a covariate adjustment, which averaged residuals for the two cover crops. Means separations for grazing (and mowing) effects were made by comparing least square means. Data were square root-transformed when necessary to meet ANOVA assumptions of equal variances. Analyses were done using SAS software v. 9.2 ProcMixed (SAS, Cary, NC, US). Unless stated otherwise, basal cover rather than canopy cover is reported because basal cover is a measure that does not vary with current defoliation levels as canopy cover does, but represents the outcome of canopy or below-ground competition in response to differential injury or sensitivity of species to defoliation or other variables that grazing may impact.

Results

Total vegetative basal cover was much higher in the native shortgrass steppe compared with either early- or mid-seral seeded grassland, even though the mid-seral field was planted 15 yr prior to the start of this study (Fig. 1). The mid-seral grassland had generally significantly higher vegetative basal cover than the early-seral field, but the means across all years were not greatly different at 11.1% and 6.3%, respectively compared to 39.3% for native grassland. Total basal cover in the early-seral grassland increased slightly through time due to grass development among a somewhat constant forb cover. Grazing effects on total vegetative basal cover were not seen for the first 2 yr of treatment in early- and mid-seral communities, but was greater in ungrazed compared with grazed treatments in both CRP fields in the third year of treatment. For both CRP fields, differences between grazing treatments in total cover were mostly due to higher grass cover in the ungrazed treatment. In contrast, total basal cover was higher in grazed rather than ungrazed native communities, and this was also due primarily to the grass component, but in opposite directions with grazing than in the seeded communities. Forbs did not respond to grazing treatments in the early-seral field or native shortgrass steppe, but decreased in the mid-seral field. Mowing compared with grazing stimulated more grass and less forb basal cover in 2 of 3 yr, resulting in no significant differences in total vegetative basal cover.

Planted grass species included the perennials *B. gracilis*, *P. smithii*, *B. curtipendula* and *B. inermis*, but since *B. inermis* was one of the targeted non-native species we statistically analysed planted native grass species (all perennials) and non-planted native perennial grass species that established in the early- and mid-seral communities from outside seed sources, with the non-native perennial *B. inermis* analysed separately below. This grouping isolates *P. smithii* in the early-seral community, because no seeded *B. gracilis* or *B. curtipendula* emerged due to periodic and extended drought conditions during the early years. The grouping primarily comprises *B. gracilis* (69% of the group) and *B. curtipendula* (30%) in the mid-seral community, because *P. smithii* establishing from nearby native fields was rare (1%). *B. gracilis* is the dominant in the native shortgrass steppe study fields (92% of the group) and *P. smithii* is an important but much less abundant component of the basal cover (8%) due to both lower abundance and upright growth form and lack of crown structure. Planted species basal cover was very low in the early-seral community and increased in the mid-seral, but the cover in the mid-seral was very much lower than in native shortgrass steppe communities (Fig. 2a). Grazing significantly increased basal cover of species in the planted group in native shortgrass steppe in two of the 5 yr (due to increases in *B. gracilis* not *P. smithii*, data not shown), and

in the mid-seral community in one of the three grazing treatment years, but had no significant effect in the early-seral community. Mowing and grazing treatments did not differ in the early-seral community for this group. Selectivity coefficients indicated that *B. gracilis* was marginally avoided and *B. curtipendula* was selected in proportion to abundance in the mid-seral community, compared to *B. gracilis* selected in proportion to abundance in the native community. *B. curtipendula* never occurring in the native shortgrass steppe in any treatments currently or previously sampled at the experimental sites. *P. smithii* was highly selected for in both the early-seral and native communities.

Important non-planted native perennial grasses included *A. longiseta*, *Carex eleocharis* Bailey, *Sitanion hystrix* (Nutt.) J.G. Sm., *Sporobolus cryptandrus* (Torr.) Gray and lesser amounts of *B. dactyloides*, *Muhlenbergia torreyi* (Kunth) A.S. Hitchc ex Bush (ring muhly) and *Schedonnardis paniculatus* (Nutt.) Trel. (tumblegrass). Basal cover of non-planted perennial native grass species was lower than planted perennial species in early-seral and especially native shortgrass steppe, but the two were of similar abundance in the mid-seral community (Fig. 2b vs 2a). Basal cover of non-planted perennial native grass species in the last two wetter years was somewhat similar between mid-seral and native communities (Fig. 2b). However, grazing

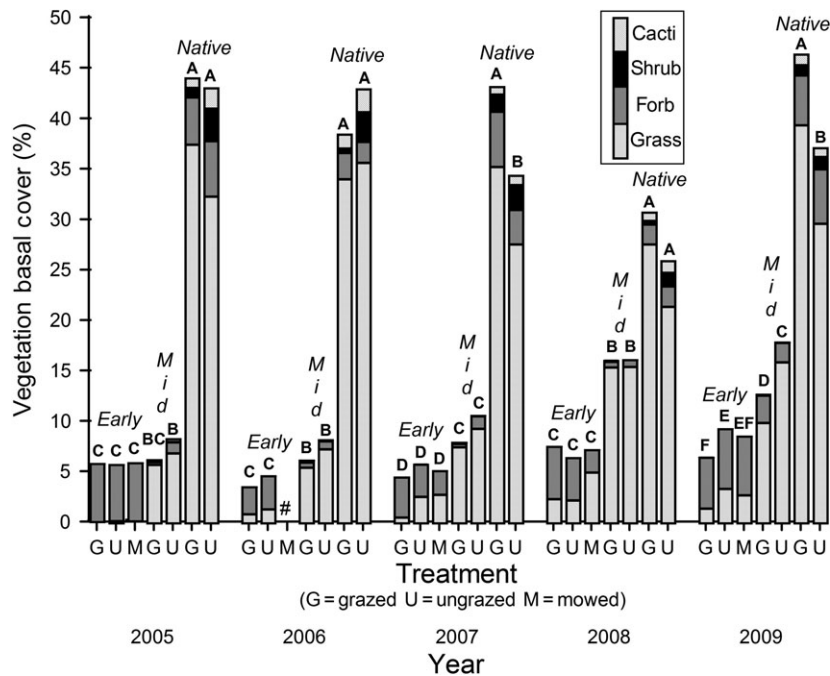


Fig. 1. Total vegetative basal cover (%) and its composition in term of grass, forb, shrub and cactus in early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed and mowed treatments for 5 yr. The first 2 yr for seeded grasslands were pre-treatment. Bars within a year not sharing a common letter are significantly different for total vegetation basal cover. Mowing was not applied in 2006 due to dry conditions and short height of vegetation. See Appendix S1 for statistics for life-form groups.

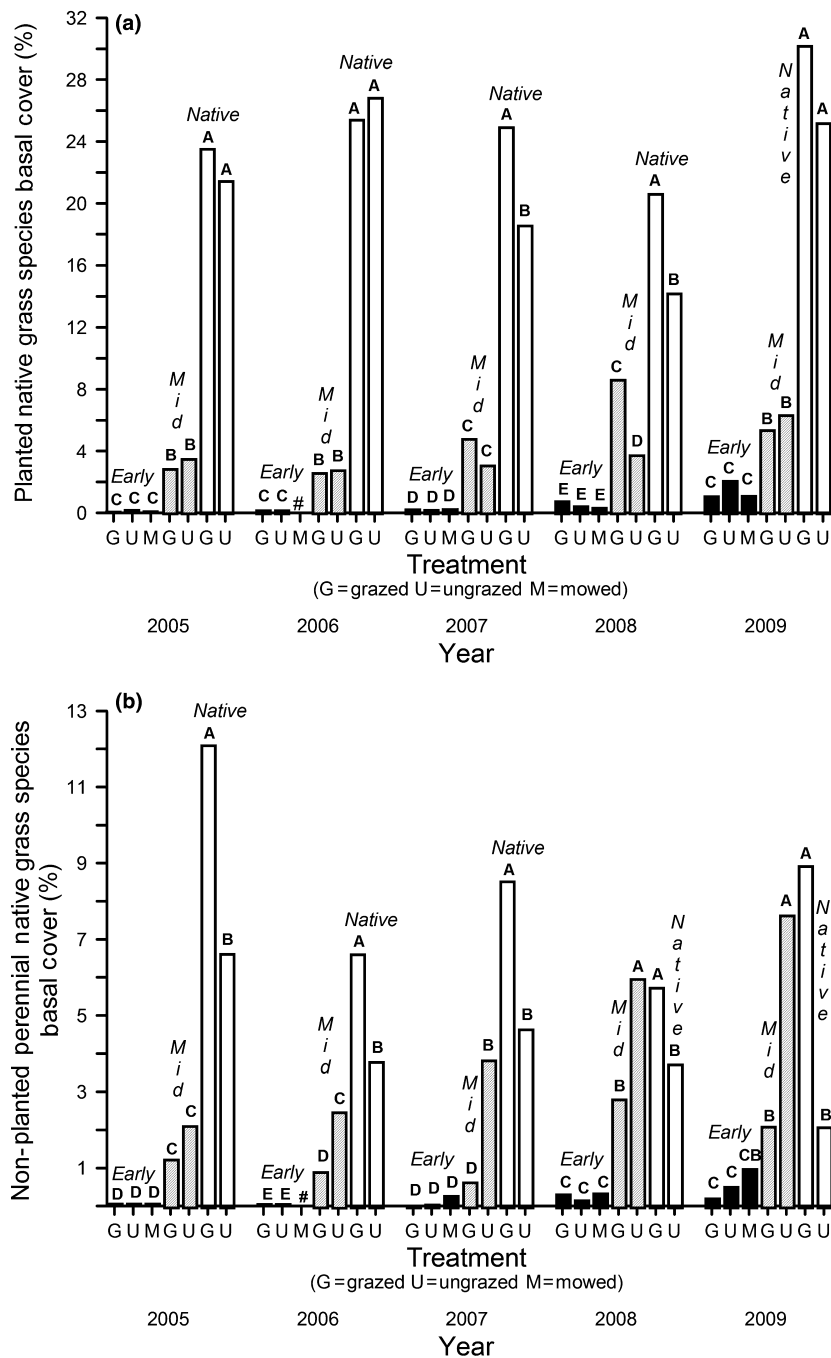


Fig. 2. Basal cover (%) of (a) planted native grass species and (b) non-planted perennial native grass species in early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed and mowed treatments for 5 yr. The first 2 yr for seeded grasslands were pre-treatment. Bars within a year not sharing a common letter are significantly different.

had opposite effects on this group in mid-seral vs native communities, and sometimes effects were large. In this case, however, differences existed in one of the pre-treatment years in the mid-seral community, but grazing magnified the difference in subsequent treatment years.

Grazing increased non-planted native perennial grass basal cover in native shortgrass steppe but decreased it in mid-seral grassland. No significant grazing or mowing effects were observed for non-planted perennial native grass species in the early-seral community. Planted and

non-planted perennial native grass species tended to increase at a similar rate through time in the early-seral community (Fig. 2a,b).

We contrast the above analyses of native perennial grass groups with invasive (weed) forb species (both annual and perennial) and target annual invasive forbs on the early-seral community and target *B. inermis* on the mid-seral community. Basal cover of invasive (weed) forb species was much more abundant on the early-seral than the other two communities, where they were generally similarly abundant (Fig. 3a). Grazing had no significant effect on invasive forb species during treatment years on either early- or mid-seral communities, whereas mowing compared with grazing reduced this group during one of three treatment years. Invasive forb species were higher on ungrazed compared with grazed native shortgrass steppe in the very productive 2009, the most abundant year for them on mid-seral and native communities. The three target annual invasive species (*K. scoparia*, *S. iberica*, *S. altissimum*) of the early-seral community fluctuated with year, did not respond to grazing pressure, but decreased with mowing compared to grazing in two of three treatment years (Fig. 3b). Cattle selected for *K. scoparia* in proportion to its abundance in the early-seral community, and this was the most abundant of target species, but the other two were selected against even though part of the grazing occurred very early in their phenology. In contrast, the *B. inermis* target species for grazing on the mid-seral community was negatively impacted by grazing in the latter 2 of 3 yr of treatment (Fig. 3c), and was selected by cattle in proportion to its abundance.

Short grass species were dominants of native shortgrass steppe, and very low in basal cover on early- and mid-seral communities (Fig. 4a). Grazed compared to ungrazed native communities generally had a much higher abundance of short grasses, and the opposite occurred for tall grasses in response to grazing (Fig. 4b). The very low basal cover of short grass species on early- and mid-seral communities did not respond to grazing or mowing treatments (Fig. 4a). In contrast, tall grass species had higher basal cover on ungrazed compared to grazed mid-seral community in two of three treatment years, and in ungrazed and mowed compared with grazed early-seral communities in one of three treatment years (Fig. 4b).

Compositional dissimilarity indices of early-seral communities were always more than 95% different to the native communities, and there were no significant differences among grazed, ungrazed or mowed communities (Appendix S1). Mid-seral communities were always from 55% to 80% dissimilar to native communities 15+ yr after successful establishment of seeded species. Community species richness of mid-seral communities was often half

that of native shortgrass steppe, and early-seral lower than mid-seral communities (Appendix S1). Grazed compared with ungrazed native shortgrass steppe was lower in diversity in 1 of 5 yr. Grazing had no significant effect on species richness of mid-seral communities, and reduced richness in 1 of 3 yr on early-seral communities.

Discussion

Recovery toward undisturbed native shortgrass steppe for various groups in the last year of this study for early- and mid-seral communities (6 and 20 yr old), respectively, was 19% and 36% for total vegetation cover, 5% and 21% for planted native species, 10% and 88% for non-planted native perennial grasses, only 0.2% and 13.0% for short grasses, with overall dissimilarity in community species compositions of 97% and 68%. This illustrates the very slow rates of secondary succession in this semi-arid grassland, and also the potential importance of non-seeded perennial grasses that may establish from outside seed sources. Non-seeded perennial grasses in the mid-seral field were the closest to the basal cover in native steppe of groups examined, and were of similar basal cover to planted native perennial grasses within the mid-seral community.

Grazing is the evolutionarily historical condition for native shortgrass steppe that evolved with bison grazing (Milchunas et al. 1988), and ungrazed communities are more similar to a variety of disturbed community types than are grazed communities (Milchunas et al. 1990). Early-seral invasive annual species are more abundant, and dominant perennial short grasses less abundant in ungrazed compared with grazed native shortgrass steppe (Milchunas et al. 1992). All species group variables examined in this study for native shortgrass steppe displayed effects of grazing that would be considered a positive seral direction based on succession models cited above, except for forbs, which were unaffected in these moderately grazed pastures (Table 1) but are also negatively impacted by heavy grazing (Milchunas et al. 2008). Thus, the moderately grazed native sites in this study generally agreed with previous studies of heavy grazing, showing that grazing maintained communities in a composition more descriptive of a late-seral stage, and ungrazed communities of a more disturbed composition. How, though, did grazing affect seral transition states of planted fields under secondary succession?

The effects of grazing treatments on successional development of abandoned fields or seeded grassland in the shortgrass steppe have not been studied, even though grazing is the primary land use of native communities (Hart 2008) and CRP is an important component of the landscape (9265 km² in Colorado), with contracts over large

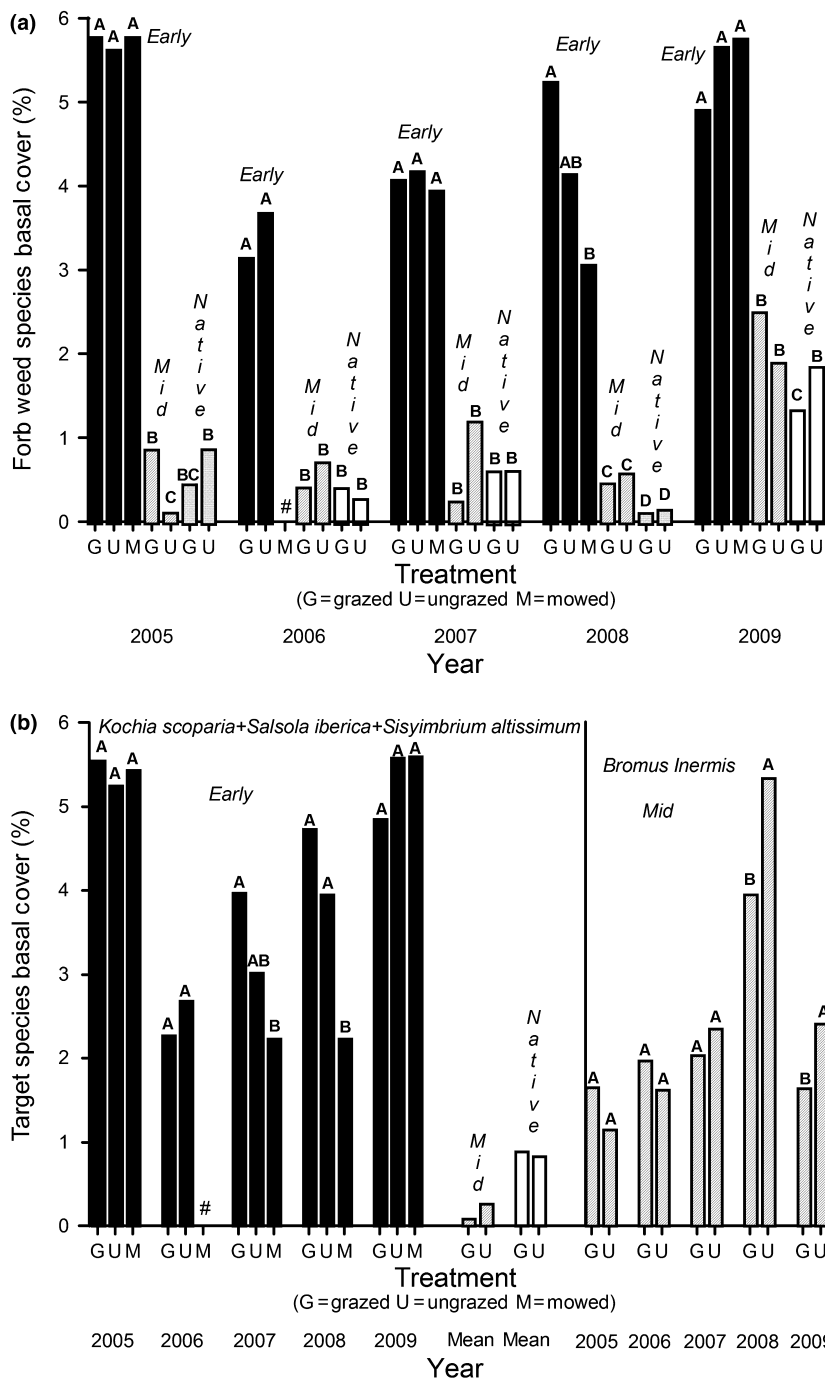


Fig. 3. Basal cover (%) of (a) invasive (weed) forb species and basal cover of (b, c) species targeted by treatments in the early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed and mowed treatments for 5 yr. The first 2 yr for seeded grasslands were pre-treatment. Bars within a year not sharing a common letter are significantly different. The three target forb species were too low for statistical analyses in mid-seral and native grassland, and the exotic seeded *Bromus inermis* was not encountered in early-seral or native grassland.

areas that have or will soon expire (Barbarika et al. 2005). Grazing management has been suggested as one of several factors possibly responsible for the large differences in rates of recovery of different fields when soil textures are simi-

lar, but there is little known about how this and other factors affect recovery rates (Coffin et al. 1996; Peters et al. 2008). We observed small effects of grazing and mowing compared to the ungrazed treatment on succession in this

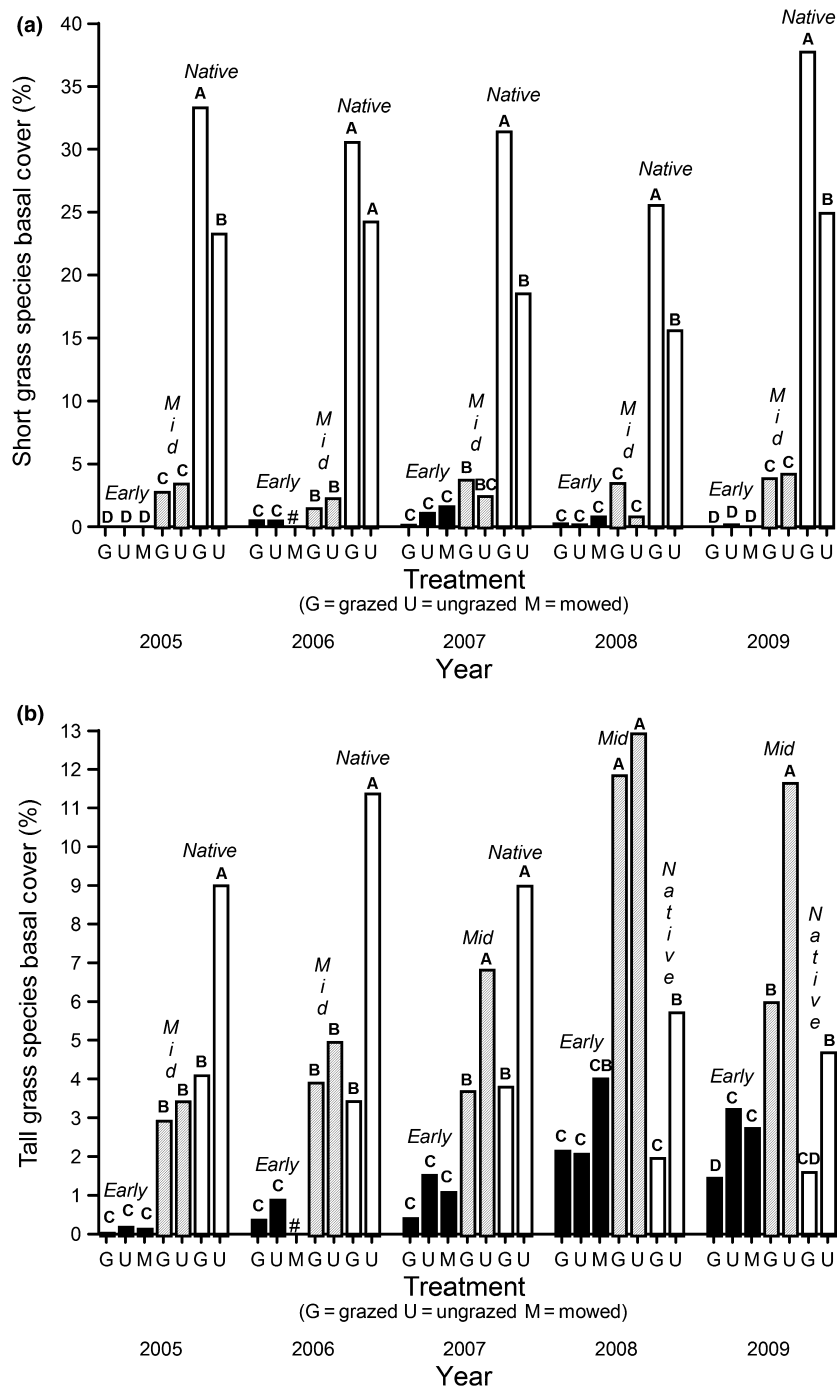


Fig. 4. Basal cover (%) of (a) short grass species and (b) tall grass species in early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed and mowed treatments for 5 yr. Heights of species were based on relative position in canopy in or in native shortgrass steppe. The first 2 yr for seeded grasslands were pre-treatment. Bars within a year not sharing a common letter are significantly different.

study when viewed at the community level (total vegetative cover, dissimilarity compared to native shortgrass steppe, and species richness), in that effects were either non-existent or small and/or occurred in conditions of 1 yr

but not others. Further, the directions of effects were mixed for mid-seral grassland (Table 1). Dissimilarity of grazed and ungrazed early-seral grassland vs native communities did not differ, but this is largely because very few

Table 1. Effects of grazing and mowing on the direction of succession in early-seral, mid-seral and native shortgrass steppe for various response variables based on succession models for short-grass, summarized from several studies in Coffin et al. (1996) and Peters et al. (2008), and modified for Conservation Reserve Program in Munson & Lauenroth (2012).

Community Variable	Effect on Direction of Succession			
	Early-Seral		Mid-Seral	Native
	Grazing	Mow vs Graze ¹	Grazing	Grazing
Dissimilarity	0	0	+	na
Species richness	? ²	? ²	0	+
Total vegetative cover	–	0	–	+
<i>Species Group Variable</i>				
Forbs	0	+	+	0
Grasses	–	+	–	+
Planted native perennial grasses	0	0	+	+
Non-planted native perennial grasses	0	0	–	+
Invasive (weed) forbs	0	+	0	+
Target species	0,+ ³	+,- ³	+	na
Short grasses	0	0	0	+
Tall grasses	+ ? ²	– ? ²	+	+

See Methods section or figures for units and methods of sampling and calculation.

¹Mowing compared with grazing effect.

²See text for interpretation.

³The positive for grazing and negative for mowing is for *B. tectorum* from canopy cover data in Milchunas (2011).

species were found in common and proportions were vastly different for species in common. The negative effect on total vegetative basal cover with grazing can be viewed as a negative effect on succession due to the potential for soil loss, which was observed during one extremely dry windy winter (pers. obs.), and because of the relatively high basal cover of the sod-like, grazing lawn structure of native vegetation. High total vegetative cover of grazed compared with ungrazed communities is a characteristic of native communities that is important in resisting both invasive establishment and soil erosion in this very windy environment (Milchunas & Lauenroth 1989; Milchunas et al. 1992). Mowing did not differ from grazing in dissimilarity of the early-seral community. Diversity is difficult to interpret in terms of succession because species lost may be native or invasive, perennial or annual, etc., but diversity showed some reductions with grazing in both native and early-seral communities and trended lower in mid-seral communities.

Grazing effects on succession in mid-seral grassland for species group variables amounted to two negative, two neutral and four positive, but again the effects were most

often not seen consistently in all years of treatment and/or were small in magnitude (Table 1). Although there was some indication that grazing reduced the target *B. inermis* and increased planted native perennials, there were no effects on invasive forbs and negative effects on non-planted native perennial grasses. Advancing beyond a composition of primarily planted native grass species would depend on this latter group, and grazing had interesting and contrasting or counterbalancing effects when viewed from native vs mid-seral communities. Grazing had consistent and relatively large positive effects on non-planted native perennial grasses in native shortgrass steppe, which would increase the potential for seed sources to adjacent seral grasslands, while on the other hand grazing had the effect of reducing this important group in the mid-seral grassland.

In contrast to mixed effects in mid-seral grassland, grazing had primarily neutral effects on basal cover of species groups in the early-seral grassland when those variables are placed in the context of successional models for the region (Table 1). There were negative effects of grazing in terms of grasses, and this may have impacts on soil erosion and development, as indicated for total vegetative cover. A positive effect on a component not included specifically in succession models was found for the exotic annual invasive *B. tectorum*, but only in 1 yr of study (Milchunas et al. 2011). The positive effect on succession by having a negative effect of grazing on tall grasses must be qualified in this case because a concomitant positive effect on short grasses was not observed, and this was due to a lack of *B. gracilis*, *Buchloe dactyloides* (Nutt.) J.T. Columbus, and *Carex* spp. in the early-seral community, which are increaser species with grazing in native shortgrass steppe communities. One important relatively tall grass in the early seral community was the seeded *P. smithii*, which is a highly palatable species to many native and domestic consumers and is a particularly sensitive decreaser species with grazing in native steppe communities (Milchunas et al. 1989, 2008; Lauenroth & Milchunas 1992). Interestingly, however, grazing did not significantly affect the abundant *P. smithii* in the early-seral matrix of species (Milchunas et al. 2011). This species responded very differently to grazing, depending on the community species composition it was growing with, even though it was highly palatable and selected for in both early-seral and native communities. Mowing compared with grazing tended to be slightly more positive in terms of succession of the early-seral community, with the exception of *B. tectorum*.

With respect to our initial hypotheses in the case of the early-seral community, we reject the hypothesis that grazing would speed succession, while generally accepting the hypothesis in the mid-seral community with some equivocation. Grazing of native shortgrass steppe communities

reduced components indicative of earlier seral stages in this study of moderate grazing, and more so in heavily grazed treatments (Milchunas et al. 2008). Therefore, we accept our alternative hypothesis as our second main hypothesis: that grazing would have different effects on succession in the three different communities. Additional years of treatment and study are necessary to fully evaluate grazing effects in these CRP fields, and studies of fields with different species compositions and soils would help assess which conditions would or would not result in speeding of secondary succession with grazing. The early-seral community in this case was not ideal for testing successional hypotheses because the seeded shortgrass steppe dominant *B. gracilis* did not establish during the dry initial conditions, and the target invasive species (*K. scoparia*, *S. iberica*, *S. altissimum* and *B. tectorum*) and perennial native grass species (*P. smithii*) that did establish are similar in season of growth and height. The three target invasive species in the early-seral field did not respond to grazing in terms of basal cover, but grazing did affect canopy cover (Milchunas et al. 2011; see Methods section caged and uncaged removal estimates). The reduction in tall grasses with grazing is a common response even at global scales (Díaz et al. 2007), and in the shortgrass steppe case indicates that less fragmentation of the landscape by the uncharacteristically tall species planted in many CRP fields in this region (Kamler et al. 2003; McIntyre 2003; Sampson et al. 2004) may be mitigated with grazing, as initially hypothesized. Decisions whether to graze may best be made only after assessing whether tolerant native short-grass species establish, and further study of early-seral communities with this component would be useful. If wildlife objectives are directed towards species associated with short-stature grassland (Milchunas et al. 1998), then grazing of similar mid-seral communities not only removes canopy cover but also moves the community towards a native short species composition that sequesters greater amounts of C below-ground than non-native tall grasses (Munson et al. 2012).

In conclusion, grazing effects on secondary succession varied with seral stage, even in this region with a long evolutionary history of grazing with grazing-tolerant late-seral species. The tolerance of individual species and groups to grazing also varied with seral stage, indicating that the community species matrix that a species or group grows within can determine responses to grazing. Further, the effects of grazing on successional trajectories sometimes varied with functional groups within a seral stage. Grazing effects were most often small in magnitude or manifest only under particular annual abiotic conditions. This may be associated with the long evolutionary history of grazing for this region, but comparisons are not possible because studies of grazing effects in multiple seral stages are lacking

for most community types (but see one example in citations in Gibson et al. 1987).

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Leonard and Tammie Ball and Roland and Verda Ball of the Ball Ranch allowed us to work on their property, provided historical information and ground support without which these experiments could not have been completed. Art Allen and Fritz Knopf (both USGS retired) were important in initial project setup. Phil Chapman provided statistical advice and Dan Manier provided reviews of early manuscript drafts. Research was funded by the US Department of Agriculture – Farm Service Agency, the Shortgrass Steppe Long-Term Ecological Research Program (National Science Foundation DEB-0217631, 0823405), and the US Geological Survey.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Seven yr of annual and monthly precipitation at the study sites (Fig. S1), plant community spe-

cies dissimilarity indices and species richness for grazing and mowing treatments over 5 yr of study (Fig. S2), and life-form statistics for paper Fig. 1.

Fig. S1. Monthly and mean annual precipitation (mm, October previous year through September current year) from 2003 to 2009 at the Briggsdale, Colorado weather station approximately 5 km southeast of study area.

Fig. S2. (A) Plant community species dissimilarity [Whittaker (1952) index (%) of community association] for early-seral and mid-seral seeded grassland grazed, ungrazed, or mowed contrasted with native grazed shortgrass steppe for 5 yr. A dissimilarity value of 100 % would mean that the two contrasted communities had no species in common, and a value of 0 % would mean that all species found in one community were found in the other and each species was observed in the same proportional abundance between the two contrasted communities. Bars within a year not sharing a common letter are significantly different. (B) Plant community species richness (or species density, number sampled per treatment-replicate-year in all quadrats) in early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed, and mowed treatments for 5 yr. The first 2 yr for seeded grasslands were pre-treatment.

Appendix S1

Milchunas, D. G., and M. W. Vandever. 2013. Grazing effects on plant community succession of early- and mid-seral seeded grassland compared to shortgrass steppe.

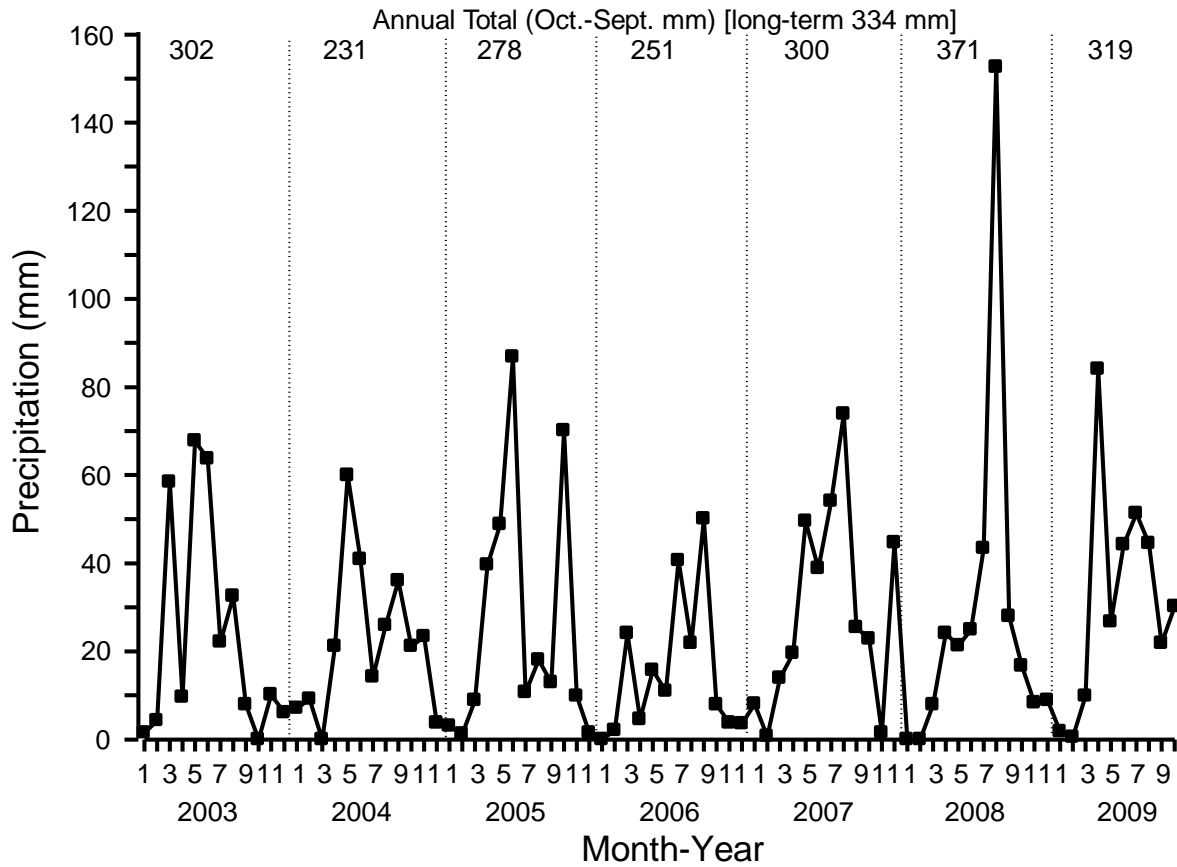


Fig. S1. Monthly and mean annual precipitation (mm, Oct. previous year through Sept. current year) from 2003-2009 at the Briggsdale, Colorado weather station approximately 5 km southeast of study area.

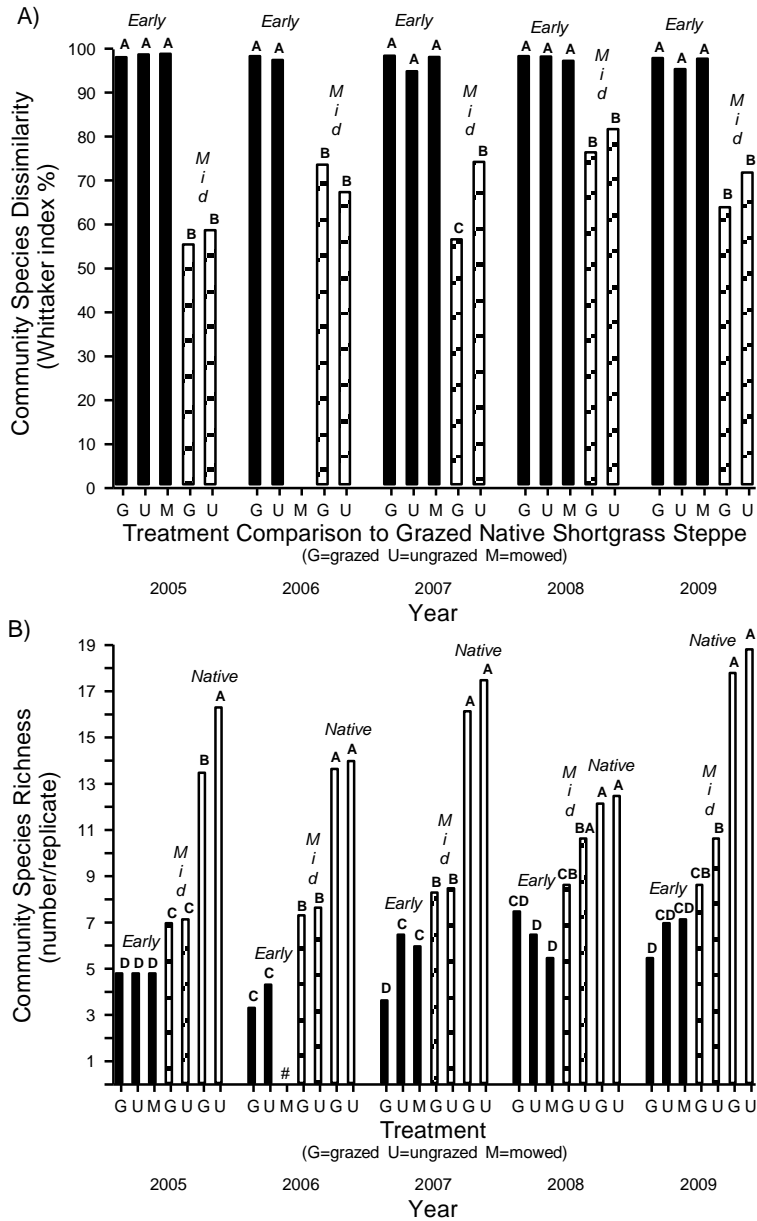


Fig. S2. A) Plant community species dissimilarity (Whittaker (1952) index (%) of community association) for early-seral and mid-seral seeded grassland grazed, ungrazed, or mowed contrasted with native grazed shortgrass steppe for 5 years. A dissimilarity value of 100 % would mean that the two contrasted communities had no species in common, and a value of 0 % would mean that all species found in one community were found in the other and each species was observed in the same proportional abundance between the two contrasted communities. Bars within a year not sharing a common letter are significantly different. B) Plant community species richness (or species density, number sampled per treatment-replicate-year in all quadrats) in early-seral and mid-seral seeded grassland and native shortgrass steppe in grazed, ungrazed, and mowed treatments for five years. The first two years for seeded grasslands were pre-treatment. Bars within a year not sharing a common letter are significantly different.

Life-form statistics for Fig. 1 in Milchunas and Vandever from SAS output.

Treatment Numbers are:

- 1=native shortgrass steppe grazed
- 2=native shortgrass steppe ungrazed
- 4=early-seral grazed
- 5=early-seral ungrazed
- 6=early-seral mowed
- 8=mid-seral ungrazed
- 9=mid-seral grazed

Grasses:

Least Squares Means for effect TreatmentNumber
Pr > |t| for H0: LSMean(i)=LSMean(j)

Dependent Variable: SquareRootGRASS

i/j	1	2	4	5	6	8	9
1		0.0468	<.0001	<.0001	<.0001	<.0001	<.0001
2	0.0468		<.0001	<.0001	<.0001	<.0001	<.0001
4	<.0001	<.0001		0.6477	0.6451	<.0001	<.0001
5	<.0001	<.0001	0.6477		0.9971	<.0001	<.0001
6	<.0001	<.0001	0.6451	0.9971		<.0001	<.0001
8	<.0001	<.0001	<.0001	<.0001	<.0001		0.3355
9	<.0001	<.0001	<.0001	<.0001	<.0001	0.3355	

Forbs:

Least Squares Means for effect TreatmentNumber
Pr > |t| for H0: LSMean(i)=LSMean(j)

Dependent Variable: SquareRootFORB

i/j	1	2	4	5	6	8	9
1		0.2420	0.1289	0.1751	0.1245	<.0001	<.0001
2	0.2420		0.7184	0.8480	0.7045	<.0001	<.0001
4	0.1289	0.7184		0.8657	0.9850	<.0001	<.0001
5	0.1751	0.8480	0.8657		0.8510	<.0001	<.0001
6	0.1245	0.7045	0.9850	0.8510		<.0001	<.0001
8	<.0001	<.0001	<.0001	<.0001	<.0001		0.0882
9	<.0001	<.0001	<.0001	<.0001	<.0001	0.0882	

Shrubs and Cacti: Not statistically analyzed due to low numbers in some treatments. Values provided only to add to 100% for Total Vegetative cover and for compositional information.