

Allelopathic Cover Crop Prior to Seeding Is More Important Than Subsequent Grazing/Mowing in Grassland Establishment

Daniel G. Milchunas,¹ Mark W. Vandever,² Leonard O. Ball,³ and Skip Hyberg⁴

Authors are ¹Research Scientist, Forest, Rangeland, and Watershed Stewardship Department, Colorado State University, Fort Collins, CO 80523-1472, USA; ²Rangeland Management Specialist, US Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526-8118, USA; ³Rancher, Ball Ranch, Briggsdale, CO 80611, USA; and ⁴Agricultural Economist, Economic Policy Analysis Staff, Farm Service Agency, Washington, DC 20250, USA.

Abstract

The effects of grazing, mowing, and type of cover crop were evaluated in a previous winter wheat–fallow cropland seeded to grassland under the Conservation Reserve Program in eastern Colorado. Prior to seeding, the fallow strips were planted to forage sorghum or wheat in alternating strips (cover crops), with no grazing, moderate to heavy grazing, and mowing (grazing treatments) superimposed 4 yr after planting and studied for 3 yr. Plots previously in wheat had more annual and exotic species than sorghum plots. Concomitantly, there were much greater abundances of perennial native grass and all native species in sorghum than wheat cropped areas. The competitive advantage gained by seeded species in sorghum plots resulted in large increases in rhizomatous western wheatgrass. Sorghum is known to be allelopathic and is used in crop agriculture rotations to suppress weeds and increase crop yields, consistent with the responses of weed and desired native species in this study. Grazing treatment had relatively minor effects on basal and canopy cover composition of annual or exotic species versus perennial native grass or native species. Although grazing treatment never was a significant main effect, it occasionally modified cover crop or year effects. Opportunistic grazing reduced exotic cheatgrass by year 3 but also decreased the native palatable western wheatgrass. Mowing was a less effective weed control practice than grazing. Vegetative basal cover and aboveground primary production varied primarily with year. Common management practices for revegetation/restoration currently use herbicides and mowing as weed control practices and restrict grazing in all stages of development. Results suggest that allelopathic cover crop selection and opportunistic grazing can be effective alternative grass establishment and weed control practices. Susceptibility, resistance, and interactions of weed and seeded species to allelopathic cover species/cultivars may be a fruitful area of research.

Resumen

Se evaluaron los efectos del pastoreo, el corte, y el tipo de cultivo acompañante en tierras sometidas a cultivo de trigo de invierno y barbecho, convertidas a pasturas permanentes a través del Programa de Reservas de Conservación en el este de Colorado. Antes de la siembra se implantó sorgo forrajero o trigo en fajas alternas (cultivo acompañante) en las franjas de barbecho; las mismas recibieron protección del pastoreo, pastoreo moderado a intenso, y corte (tratamientos de pastoreo) superpuesto cuatro años después de la siembra y fueron estudiadas por tres años. Las parcelas en las que se implantó trigo tuvieron más especies anuales y exóticas que las parcelas implantadas con sorgo. De modo concomitante, la abundancia de pastos perennes nativos y de todas las especies nativas fue mayor en las parcelas de sorgo que en las de trigo. La ventaja competitiva de las especies implantadas en parcelas de sorgo dieron lugar a un gran incremento de la especie rizomatosa *Pascopyrum smithii*. El sorgo tiene propiedades alelopáticas conocidas y se usa en rotaciones de cultivos agrícolas para suprimir malezas y aumentar el rendimiento de los cultivos, en consonancia con las respuestas de malezas y especies nativas deseadas en este estudio. El tratamiento de pastoreo tuvo efectos relativamente menores en la cobertura basal y de canopeo de especies anuales o exóticas vs. pastos perennes nativos o especies nativas. Aunque el tratamiento de pastoreo nunca fue un efecto principal significativo, ocasionalmente modificó los efectos del cultivo acompañante o del año. El pastoreo oportunista redujo el pasto exótico *Bromus tectorum* al tercer año del estudio, pero también redujo a la especie nativa palatable *P. smithii*. El corte fue una práctica de control de malezas menos efectiva que el pastoreo. La cobertura vegetativa basal y la productividad primaria aérea variaron principalmente con el año. Prácticas de manejo comunes para revegetación/restauración actualmente utilizan herbicidas o corte como método de control de malezas, y restringen el pastoreo en todas las etapas de implantación. Estos resultados sugieren que un cultivo acompañante con propiedades alelopáticas y el pastoreo oportunista pueden ser prácticas alternativas efectivas de control de malezas. La susceptibilidad, resistencia, y las interacciones de malezas y especies cultivadas a las especies/cultivares de cultivos acompañantes con propiedades alelopáticas podría ser un área de investigación fructífera.

Key Words: Conservation Reserve Program revegetation, exotic weed suppression, opportunistic grazing, priority effects from soil legacy, restoration succession, sorghum allelopathy

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Correspondence: Daniel G. Milchunas, Forest, Rangeland, and Watershed Stewardship Department, Colorado State University, Fort Collins, CO 80523-1472, USA. Email: Daniel.Milchunas@Colostate.edu

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INTRODUCTION

Allelopathic crop species have gained attention for their ability to reduce weed species growth in crop agriculture settings (Singh et al. 2003), but little is known about their potential use in native plant community restoration. Weed species control without herbicides in cropland is attained through crop rotation, cover cropping (smother cropping), and companion

cropping or polyculture (Khanh et al. 2005). There are ecological and economic implications for reducing herbicide usage (Liebman and Dyck 1993), especially where intensive agriculture practices are not practical, as in semiarid and arid rangelands. The use of allelopathic crop species prior to rangeland seeding could potentially speed recovery and increase carbon sequestration capacity by favoring late seral perennial species with greater belowground allocation compared with weedy annual species. The effect would be similar to grazing in some native grassland (Milchunas et al. 2005c) where intensively rooted shortgrass species can be favored over aboveground allocating annual exotic species (Milchunas et al. 1992). Opportunistic grazing and mowing may also be economical management options for weed species control in some rangelands.

Allelopathy has long been recognized to influence plant–plant interactions in natural communities (reviewed in Kruse et al. 2000). In contrast to weed species control, the persistence of some exotic species in plant associations and in their capacity for invasion can be tied to allelopathy (Callaway and Aschehoug 2000; Prati and Bosdorf 2004; Abhilasha et al. 2008; Bainard et al. 2009). Exotic species can create soil legacies that affect germination of subsequently sown native species (Grman and Suding 2010). In other cases, cover crops (or smother crops) have been planted simultaneously with the desired and weed species to directly compete, but competition is often not sufficiently selective with the weed species (Perry et al. 2009 and citations therein). In some communities, allelopathic species can inhibit exotic or early seral species or otherwise speed natural successional pathways. Rice (1984) hypothesized that succession was more rapid in abandoned Oklahoma and Kansas fields because prairie threeawn (*Aristida oligantha* Michx.) was tolerant to allelochemicals produced by early seral weed species. Similarly, allelochemicals produced by ragweed (*Ambrosia artemisiifolia* L.) inhibited germination and growth of first-seral stage annual species in second-seral stage soils, thereby speeding succession between the two stages (Jackson and Willemssen 1976). However, the use of allelopathic cover crops as a management tool in native plant revegetation of Conservation Reserve Program (CRP) or restoration of abandoned cropland is nonexistent as far as we know.

Sorghum has particularly high allelopathic properties from root exudation and root and stem residual biomass (Cheema et al. 2007). The use of sorghum for weed reduction has been documented in rotations with irrigated wheat (Cheema and Khaliq 2000), barley (Urbano et al. 2006), corn, mungbean, Brassica, and other crop species (Kruse et al. 2000; Cheema et al. 2004), and harvests often increased (reviewed in Liebman and Dyck 1993). Weed species control can range as high as 75% for sorghum cover crops (Urbano et al. 2006) and 40–50% for chopped herbage incorporated into soil (Cheema and Khaliq 2000). Cultivars vary in the amount of allelopathic compounds produced (Czarnota et al. 2003; Singh et al. 2003), and, similarly, various weed and crop species display differential or no susceptibility to specific allelochemicals (Labrada 2008). Sorghum is only one of many potentially allelopathic crop species with varying toxicity levels, and wheat, alfalfa, sunflower, buckwheat, and others also show some degree of allelopathy (Singh et al. 2003; Khanh et al. 2005; Belz 2007).



Figure 1. View down boundary line of former sorghum (left) and wheat (right) cover crop strips that simultaneously occupied the field in the same year prior to seeding to a native grass and forb species mix under the Conservation Reserve Program. The tall light-colored grass on the sorghum side is western wheatgrass, and darker-colored kochia dominates the wheat side. Photo was taken in late summer 2009 during the sixth growing season after seeding.

In an ongoing study of grazing effects on rangeland succession in newly planted CRP fields, we observed differences in weed species composition and especially of native perennial grass species establishment attributable to whether the previous crop was wheat or sorghum (Fig. 1). In the year prior to CRP seeding, wheat had been planted as usual, but forage sorghum had also been planted and cropped simultaneously rather than leaving half the land fallow, similar to row-crop systems adopted by some farmers in this area that are replacing the traditional wheat–fallow system with a sorghum–fallow–wheat rotation. This planting strategy suppresses weed species and can, under favorable conditions, obtain two dryland crops in a 3-yr cycle (Baumhardt et al. 2009).

Our objective here is to document a potential range management/revegetation use of crop allelopathy in improving establishment of perennial grass species in rangeland restorations and the implications for aboveground net primary production (ANPP). We pose this as an example that may stimulate further research into a little-explored area. A second objective is to assess whether grazing (or mowing) of early seral communities may also be used as a weed management option in a region with a long evolutionary history of grazing where grazed late seral native communities contain lower abundances of annual and exotic species than ungrazed communities (Milchunas et al. 1988, 1989, 1992). Mowing is often prescribed as a weed management option when regulations prohibit grazing, but responses to unselective mowing can differ from selective defoliation by grazing animals. Both cover crop choice and grazing are low-cost management options for restoration revegetation of disturbed land and previously cropped CRP. We assess these treatments by direct side-by-side contrasts of responses by groups and individual species representing weedy or exotic early seral versus long-lived native late seral conditions and how these differences manifest in terms of ANPP.

METHODS

The study area comprises CRP fields located in shortgrass steppe of north-central Colorado (Lauenroth and Milchunas 1992), approximately 5 km northwest of Briggsdale. Mean annual precipitation is 334 mm, with a standard deviation of 98 mm. Approximately 71% of the precipitation occurs during the May through September growing seasons. Mean monthly air temperatures range from 22°C in July to below 0°C in January. Soil at the site is a mix of Platner loam (Aridic Palenstoll) and Renohill fine sandy loam (Ustollic Haplargids). Native vegetation surrounding these CRP fields is dominated by blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths) and plains pricklypear cactus (*Opuntia polyacantha* Haw.), with western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve) and scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) as important components and scattered fourwing saltbrush (*Atriplex canescens* [Pursh] Nutt.) shrubs.

A 130-ha field, previously in a long-term winter wheat-fallow system, was in 2003 growing winter wheat as usual (planted previous year in September, Scout variety) plus a forage sorghum cover crop (planted in June, variety Cane X) in what would have been the fallow strips. Both crops were harvested in 2003 prior to planting to CRP in December. The wheat was harvested just after senescence in mid-July and the sorghum while still green in early September before a hard frost. However, volunteer winter wheat from residual seed appeared after harvest and was sprayed with glyphosate in November (to prevent competition with seeded species the following spring and to prevent transpiration over winter). Thus, transpiration and N uptake occurred into autumn in both cropped strips. Precipitation from September through November in 2003 was well below average at only 18 mm (long-term mean = 60 mm).

The previously alternating strips (each approximately 50 m wide) of wheat and sorghum were simultaneously seeded with a mix comprised of western wheatgrass (30%), blue grama (20%), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.; 20%), green needlegrass (*Nassella/Stipa viridula* [Trin.] Barkworth; 10%), switchgrass (*Panicum virgatum* L.; 10%), and purple prairieclover (*Dalea purpurea* Vent.; 10%) drilled to a depth of 1.27 cm (at a total PLS [pure live seed] rate of 4.8 lb·acre⁻¹ [5.38 kg·ha⁻¹]). This field is surrounded by native shortgrass steppe on three sides and by an established, midseral CRP field planted in 1989 on the other side.

Water and fencing for cattle were constructed during the early establishment period of the newly planted field, with the field divided into ungrazed, heavily grazed, and lightly grazed pastures (Fig. S1, available at <http://dx.doi.org/10.2111/REM-D-10-00117.s1>). Water was centrally placed between the two grazed treatments. We realize that the pseudoreplicated nature of the field layout imposed by limited funding for fencing limits our conclusions to this particular field. During layout of six replicate plots of each of the grazing treatments, we observed the differential native plant establishment and weed growth and composition on the previously alternating strips of wheat or sorghum (see Fig. S1, aerial photo taken during second growing season after CRP planting). Six randomly located plots (10 × 20 m), three each within a previous sorghum and wheat strip, were established to control for this variability in the

grazing study across the uniformly seeded field. All plots were ungrazed until 2007 (three ungrazed years after planting before grazing). Grazing treatments from 2007 to 2009 included ungrazed and moderate to heavily grazed treatments and additional annually mowed plots established adjacent to each ungrazed plot. Lightly grazed plots were sampled only in 2009 as an additional location/treatment conformation for this field design. Therefore, there were a total of 4 grazing treatments × 2 cover crops × 3 replicates = 24 plots within which quadrat sampling occurred. Except when indicated specifically as “lightly grazed,” the “grazed treatment” throughout the text refers to the moderate to heavily grazed condition.

Grazing treatments were applied opportunistically based on different objectives for the new and old fields, with some constraint due to proximity to the landowner's house and early/late season rotations between US Forest Service and private land. Objectives were to flash graze (intense, short period) early spring to set back the canopy development of kochia (*Kochia scoparia* [L.] Schrad.), Russian thistle (*Salsola iberica* [Sennen & Pau] Botsch. ex Czerep.), and other dominant early annual forbs and patches of cheatgrass (*Bromus tectorum* L.) before western wheatgrass was largely available and then flash graze again late in the growing season after boot stage. These objectives were met within the constraints of weather. There was no spring grazing in 2008 because of very dry conditions, and spring grazing was a little later than desired in 2007. Stocking rates in the moderate to heavily grazed treatment were approximately 4.6 AU·ha⁻¹ over 2 d in the early growing season period (using cow-calf pairs and one bull) in 2007 and 2009. Stocking rates in the moderate to heavily grazed treatment in the late season period were higher, especially in 2008 and 2009. In 2007, late season grazing was approximately the same AU·ha⁻¹ but over a 3-d period. The very heavy grazing in the 2008 and 2009 late period was approximately double (9.5 AU·ha⁻¹) over 3.5 and 4 d, respectively. Thus, we term this grazing treatment “moderate to heavy” because of the very heavy grazing in these later periods in what otherwise was considered moderate stocking. Stocking in the lightly grazed treatment for both early and late periods was approximately half that of the early season rates for the moderate to heavy treatment but occurred over more days of grazing. One mowing treatment per year was accomplished using a gas-powered nylon blade trimmer at a height of approximately 10 cm when kochia and Russian thistle were approximately 20–25 cm high.

Sampling within each plot included plant basal and canopy cover, aboveground net primary production, and estimates of grazing intensity. Basal and canopy cover were estimated at the same locations visually using 20 Daubenmire quadrats (0.1 m²) randomly located in each replicate of each treatment each year (480 total quadrats·yr⁻¹). Cover percentages were estimated by 1% increments up to 10% and by 5% increments above 10%. Aboveground net primary production at two locations for each replicate of each grazing treatment (48 total quadrats·yr⁻¹) was estimated by clipping total recent-dead-plus-live vegetation in 0.3-m² quadrats (100 × 30 cm) at a height just above grass-crown level in early autumn at peak-standing crop of current-year growth. Clipped quadrats in grazed treatments were located under movable cages (1.23 m², made from large 15-cm mesh concrete reinforcing wire) to

prevent consumption by cattle and were relocated randomly each spring to prevent snow capture effects. Vegetation was oven-dried at 55°C and weighed. Percent consumption by cattle was estimated visually as the difference in vegetation outside and adjacent to each cage compared with the quantity inside the cage before clipping. All quadrat data were averaged to replicate level prior to statistical analyses.

Data were subjected to a repeated-measures analysis of variance where the effects of years were modeled by linear and quadratic orthogonal polynomials. Interactions of grazing treatment and cover crop with the repeated measures were tested by interactions between the linear or quadratic polynomial coefficients. Tukey mean separations were calculated at either $P = 0.05$ or $P = 0.01$. Only highest-order significant interactions or main effects are presented, as are nonsignificant main effects if that treatment was not found significant at any level.

RESULTS

Precipitation from the nearby Briggsdale weather station for the period from the year prior to seeding of the CRP fields through the years of sampling in this report were 302, 231, 278, 251, 300, 371, and 319 mm · yr⁻¹ for 2003 through 2009, respectively, for a year calculated on the basis of postsenescence through the end of the growing season (previous year's October through given-year September). The year of seeding and the years following were therefore generally dry (long-term mean = 334 mm · yr⁻¹), with a few near-average years of precipitation later among them. The 3 yr of study reported here (2007–2009) had both high and very low years of ANPP relative to long-term means (Milchunas et al. 1994). The monthly distribution of precipitation during the 2007 growing season was good, with no prolonged periods of drought, even though annual total was below average. Although 2008 had above-average mean precipitation, the spring through early summer was a period of drought, followed by very heavy rains in late summer. The wet conditions of late 2008 continued through the first half of the 2009 growing season, producing good early production and an unusually good flowering/seed-head production year.

Estimated levels of consumption in the grazed treatment for 2007 were 60% ± 13 (SD) in sorghum cover crop areas and 58% ± 19 (SD) in wheat cover crop areas (SD = standard deviation of sampling estimate, i.e., same as standard error). This compared with consumption estimates of 51% ± 9 (SD) in adjacent native shortgrass steppe in a US Forest Service allotment. Grazing was deferred in 2008 until late in the year because of early drought conditions, so clipping of movable-cage plots had already occurred, and estimates of consumption based on caged versus uncaged biomass would not be meaningful. Grazing intensities in 2009 were estimated as 33% ± 21 (SD) on the sorghum and 45% ± 23 (SD) on the wheat cover crop treatments. Grazing intensities varied among years but were generally similar between cover crops.

Annual species made up the largest proportion of canopy cover on all treatments in all years. Annual species had a lower abundance on the strips of the newly seeded fields previously planted to the sorghum cover crop compared to the strips previously planted to wheat (Fig. 2A; cover crop main effect

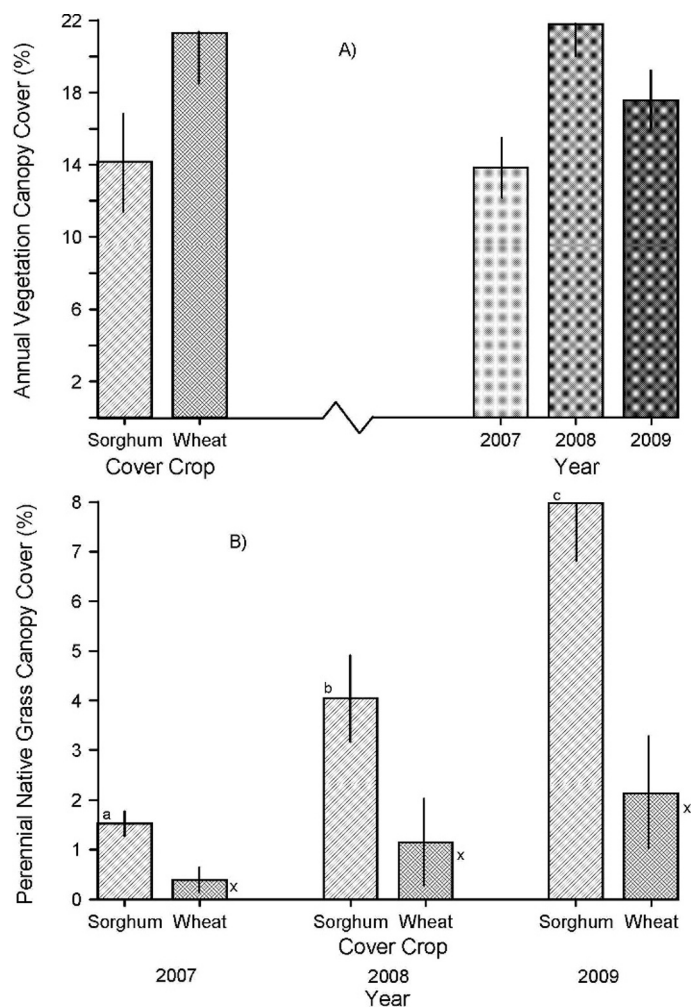


Figure 2. Canopy cover (%) of annual plant species (A) and perennial native grass species (B) in previously planted sorghum (S) or wheat (W) cover crops, ungrazed (U), grazed (G), and mowed (M) treatments, during 2007–2009 in fields seeded to native species germinating in 2004. Confidence interval lines for B are for cover crop, while means not sharing common letters within a cover crop or grazing treatment indicate significant difference between years. Broken X-axis represents separate main or interaction effects. NS = nonsignificant. Truncated confidence interval lines for tall means represent lowest half only.

$P = 0.019$). Cover of annual species varied with year in response to amounts of precipitation received (year main effect $P = 0.013$). No significant grazing treatments effects were observed as either main effects or interactions with cover crop or year (lowest $P = 0.26$). A cover crop × year interaction ($P = 0.007$) was observed for perennial native grass species canopy cover. In direct contrast to annual species, perennial native grass species canopy cover was greater ($P = 0.007$) in sorghum compared to wheat cover crops (Fig. 2B). This difference between cover crops in perennial native grass species was maintained over the 3 yr, with a sorghum/wheat abundance ratio of 3.9, 3.5, and 3.7 for 2007, 2008, and 2009, respectively. Perennial native grass species increases were increasingly greater each year on plots previously planted to sorghum, but increases on wheat plots were of a nonsignificant magnitude, and this compared to a decrease in annual species from 2008 to 2009 on both cover crops. Grazing was not a

significant factor in perennial native grass species canopy cover at any level. Basal cover of annual species produced results similar to those for canopy cover (data not shown). Perennial native grass species basal cover analyses differed from canopy cover in that a grazing treatment \times year interaction was seen in a quadratic model ($P = 0.019$), but grazing treatment was never significant in any separate year analyses (lowest $P = 0.2$).

A three-way interaction ($P = 0.038$) for exotic weed species was observed among cover crop, grazing treatment, and year. A total of 15 exotic weed species were sampled across all treatment years, with kochia, Russian thistle, tall tumble mustard (*Sisymbrium altissimum* L.), and stinkgrass (*Eragrostis cilianensis* [All.] Vign. ex Janchen) among the most abundant. Exotic species were more abundant in wheat compared to sorghum cover crops in all years (Fig. 3A). In general, grazed and mowed treatments had similar abundances of exotic species. Ungrazed compared with grazed treatments displayed some variation through time in the cover of exotic species, with some treatment/periods having greater exotic species cover in the ungrazed compared with grazed treatment. The canopy cover of native species (16 total species including all functional groups) showed an interaction between cover crop and year ($P = 0.01$) and between grazing treatment and year ($P = 0.05$). Again, in direct contrast to exotic species, the cover of native species was significantly greater in sorghum versus the wheat treatment in each year, and the amount of cover increased in all years for the sorghum treatment (Fig. 3B). Native species cover increased significantly on the wheat treatment between 2007 and 2009 but 2008 was not significantly different from either year. Increases through time had a greater positive slope in sorghum than wheat cover crops but were generally linearly increasing through time in both.

Grazing treatments did not significantly affect native species cover as a main effect ($P = 0.72$) or within any particular year (lowest $P = 0.32$), but the trajectories through time differed ($P = 0.05$). The ungrazed treatment had a greater increase in native species from the beginning to the ending year of sampling than did the grazed treatment (Fig. 3B).

Because grazing and mowing are removing canopy of both exotic and native species cover and both vegetation types showed some reductions with grazing, we calculated a native/exotic species abundance index as a measure of how potential management options compared (higher ratio numbers indicate greater abundance of native relative to exotic species). Native/exotic species coefficients were similar among grazing treatments (ungrazed = 0.182, grazed = 0.154, mowed = 0.146) but were vastly different between cover crops (sorghum = 0.334, wheat = 0.058). Basal cover analysis for exotic species showed cover crop ($P = 0.002$) and year effects ($P = 0.004$; data not shown), with the same direction of responses as observed in the three-way interaction for canopy cover. Native species basal cover and canopy cover analyses were similar.

We report here on only two individual species: cheatgrass and western wheatgrass. Cheatgrass is an exotic invasive annual weed species. Cheatgrass basal cover rather than canopy cover is shown here because of the degraded nature of the canopy of this early, cool-season species by the time of late summer sampling of the treatments. Cheatgrass abundance varied with year ($P = 0.012$). Individual year analyses indicated that abundances differed with both cover crop ($P = 0.033$) and

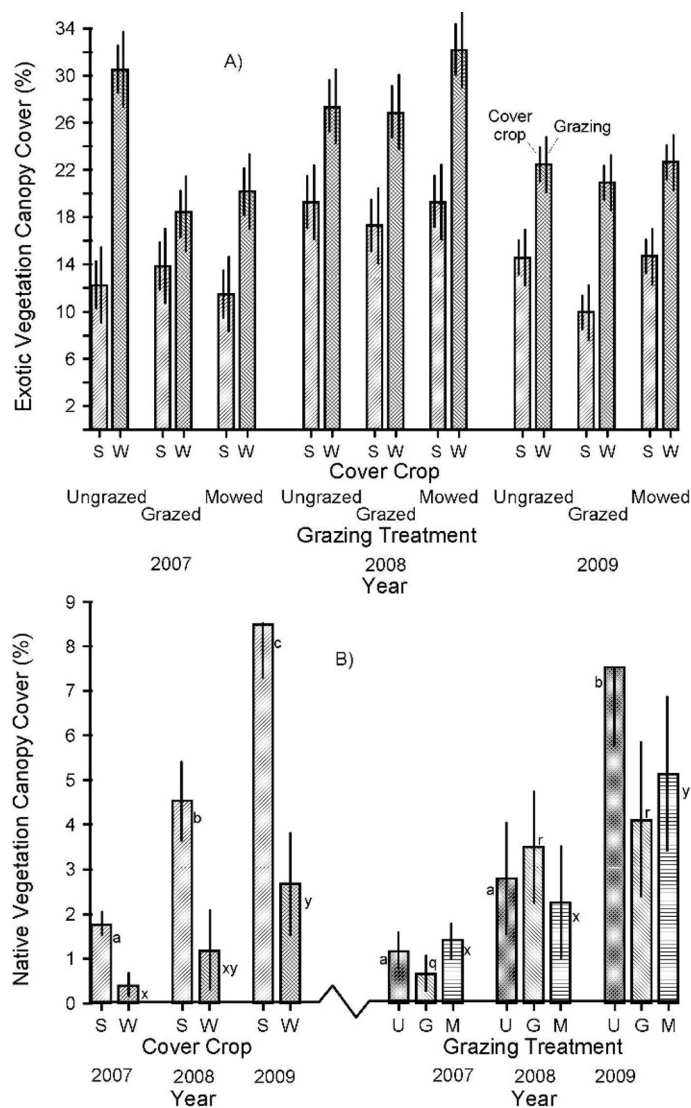


Figure 3. Canopy cover (%) of exotic plant species (A) and native species (B) in previously planted sorghum (S) or wheat (W) cover crops, ungrazed (U), grazed (G), and mowed (M) treatments, during 2007–2009 in fields seeded to native species germinating in 2004. Exotic species confidence intervals for years are not shown for simplification but are similar in magnitude to grazing treatment intervals. Confidence interval lines for B are for cover crop (left-half graph) or grazing treatment (right-half graph), while means not sharing common letters within a cover crop or grazing treatment indicate differences between years. See Figure 2 for other notes.

grazing ($P = 0.002$) in 2009. Cheatgrass basal cover was greater in wheat than sorghum cover crops and in ungrazed compared with grazed treatments (Fig. 4A). Statistical analyses of cheatgrass are hampered by the clumped distribution of near monoculture patches in many instances in this early seral stage community, leading to greater variances relative to most other species. However, the consistent patterns among treatments across all years lend support to the significant results observed in 2009.

Western wheatgrass was the most abundant native perennial grass species and was a component of the seeding mix. Cover crop interacted with year ($P < 0.001$) for western wheatgrass canopy cover. Western wheatgrass was more abundant in

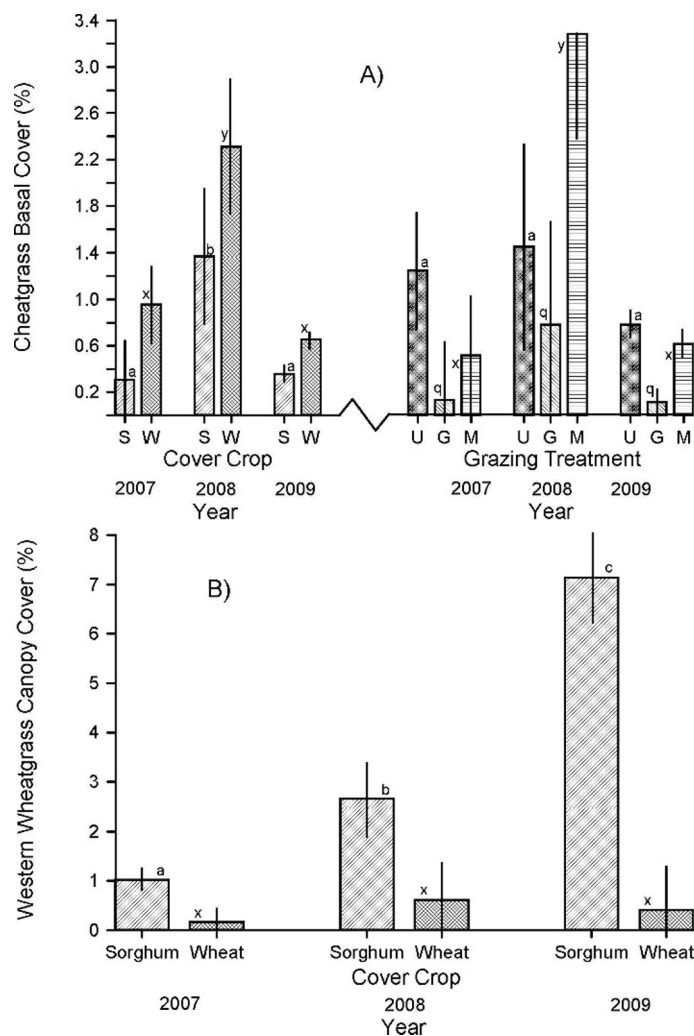


Figure 4. Canopy cover (%) of cheatgrass (**A**) and basal cover (%) of western wheatgrass (**B**) in previously planted sorghum (S) or wheat (W) cover crops, ungrazed (U), grazed (G), and mowed (M) treatments, during 2007–2009 in fields seeded to native species germinating in 2004. Confidence interval lines for **A** are for cover crop (left-half graph) or grazing treatment (right-half graph), while means not sharing common letters within a cover crop or grazing treatment indicate differences between years. See Figure 2 for other notes.

previous sorghum than wheat cover crop in all years (Fig. 4B). Canopy cover of clonal rhizomatous western wheatgrass more than doubled each year when seeded in previous sorghum strips, whereas its abundance did not significantly change with time when seeded in previous wheat strips. Grazing was not a significant factor in western wheatgrass abundance. Basal cover of western wheatgrass displayed the same statistical dynamics as canopy cover (data not shown).

Total vegetative species basal cover increased each year ($P < 0.001$) in a linear fashion (Fig. 5A). No main or interaction effects involving cover crop or grazing treatment were observed (lowest $P = 0.16$ and 0.22 , respectively). Litter basal cover varied as a function of cover crop by year ($P = 0.001$) and grazing treatment by year ($P = 0.001$). Litter was greater in wheat than sorghum planted strips in 2007 (Fig. 5B). A pattern of decreasing litter through years on wheat strips versus increasing on sorghum strips resulted in no

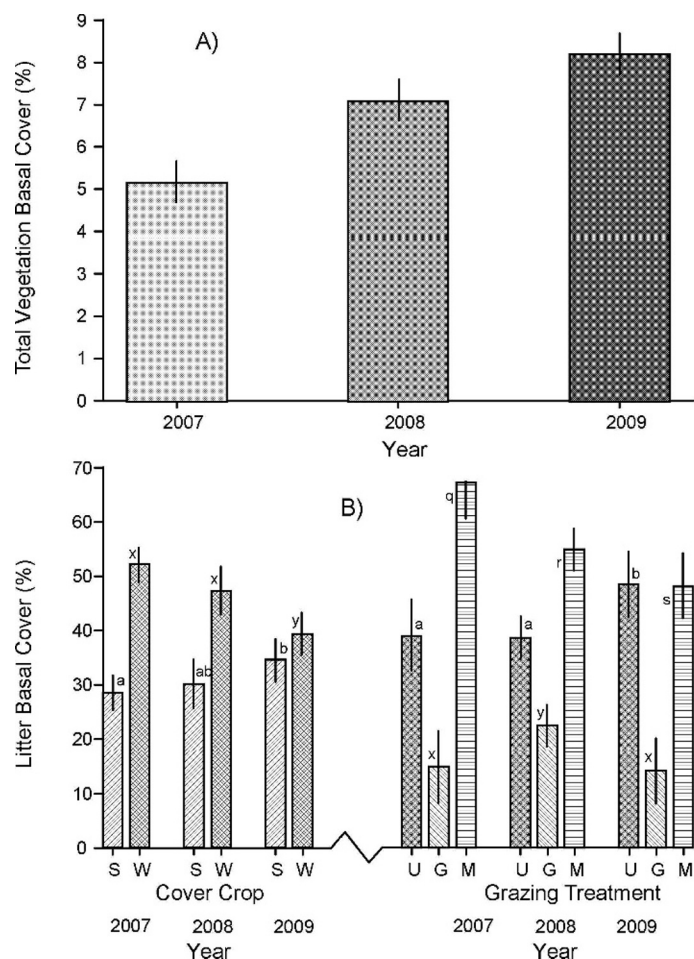


Figure 5. Basal cover (%) of total vegetation (**A**) and litter (**B**) in previously planted sorghum (S) or wheat (W) cover crops, ungrazed (U), grazed (G), and mowed (M) treatments, during 2007–2009 in fields seeded to native species germinating in 2004. Confidence interval lines for **B** are for cover crop (left-half graph) or grazing treatment (right-half graph), while means not sharing common letters within a cover crop or grazing treatment indicate differences between years. See Figure 2 for other notes.

difference between cover crops by 2009. Litter on grazing treatments was of the order mowed > ungrazed > grazed in all years, but directional changes with time differed among treatments. Mowed treatment litter decreased with time, ungrazed litter increased by the last year of sampling, and grazed litter remained unchanged between the first and the last year. Bare ground cover (data not shown) displayed the same interactions as litter but the mirror-opposite pattern in means with respect to cover crop and grazing treatments.

ANPP varied greatly with year ($P < 0.001$), illustrating the drought conditions during much of early 2008 and the lack of drought periods during the 2007 and 2009 growing seasons (Fig. 6). The heavy late-season rains that increased the mean annual precipitation for 2008 fell too late in the growing season—and just before our clipping time—for plants to respond. Averaged across all treatments, ANPP was thus 344 , 71 , and $279 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and precipitation was 300 , 371 , and $319 \text{ mm} \cdot \text{yr}^{-1}$ for 2007, 2008, and 2009, respectively. Grazed

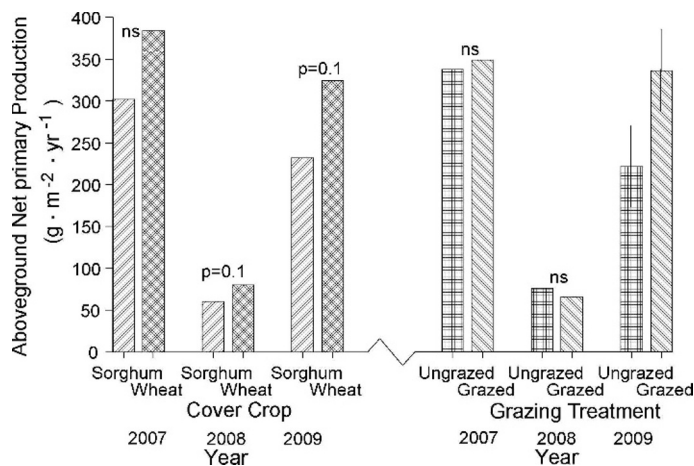


Figure 6. Aboveground net primary production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) in previously planted sorghum or wheat cover crops, ungrazed and grazed treatments, during 2007–2009 in fields seeded to native species germinating in 2004. Broken X-axis represents two separate interaction effects. NS = nonsignificant.

native shortgrass steppe ANPP displayed a similar relationship with precipitation, averaging 191, 37, and 151 $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for the 3 yr, but was always less than the CRP field means. Although ANPP ranged widely during the 3 yr of measurement, there were few significant treatment effects. ANPP tended to be greater in the previous wheat than sorghum cover crops, and the grazed treatment was more productive than the ungrazed only in 2009.

Sampling was conducted in 2009 in separate lightly grazed areas to further test cover crop and grazing treatment effects at three additional replicate locations farther from the grazing treatment locations described above. Results in all cases supported the direction and magnitude of sorghum versus wheat cover crop effects and the relatively minor effect of grazing (data not shown). In general, light grazing was more similar to the ungrazed than the moderate to heavily grazed treatment.

DISCUSSION

Although this study was originally designed to examine the effect of grazing treatments, analyses reveal that the previous crop had much greater effect on establishment and early seral development than did grazing. Planting after a wheat crop lead to a 50% increase in annual species and a 67% increase in exotic species compared to the sorghum treatment. In direct contrast, planting after sorghum resulted in a 245% increase in cover of native species, a 270% increase in perennial native grass species cover, and an 811% increase in western wheatgrass, the most abundant species from the seed mix, as compared to the wheat treatment. Soil disturbance and high nitrogen availability associated with tillage results in very large increases in weedy annual species such as kochia and Russian thistle in this region even compared to plots with competitors removed but not tilled (Milchunas et al. 1992). The initial reduction of weedy exotic annual species by the allelopathic

sorghum cover crop was mirrored by low but significantly greater establishment of rhizomatous western wheatgrass and short-lived but perennial native midseral grass species. This initial advantage for native perennial species establishment during a drought-limited germination period was followed by increasingly greater contrasts between cover crop plant community compositions with time. These results are consistent with priority effects due to soil legacies, which have the potential to change successional trajectories (Grman and Suding 2010).

Grazing was not significant as a main effect for the variables examined, although it sometimes modified cover crop and yearly weather effects. Grazing is often observed to be less important than annual weather in plant community dynamics in semiarid systems (Milchunas et al. 1994; Gillen et al. 2000; Vermeire et al. 2008). Annual species, which are particularly sensitive to weather, were not increasing because of succession and showed a +57% change from 2007 to 2008 and a –19% change from 2008 to 2009. These year-to-year dynamics compare to differences between sorghum and wheat cover crops of 41% in 2007, 43% in 2008, and 68% in 2009. In this case, cover crop within a year was generally more important in determining abundances of a dynamic, weather-sensitive plant component than between-year fluctuations, which reflected dry and wet conditions.

In the shortgrass steppe system with a long evolutionary history of grazing by bison, grazing of native grassland by cattle reduces abundances of exotic and early successional species compared with long-term ungrazed native grassland (Milchunas et al. 1992, 2008). A hypothesis in the broader context of this experiment was that grazing may be used to speed succession by favoring grazing tolerant native shortgrasses that are poor competitors in tall canopies of weedy species (Milchunas et al. 2005c). In general, grazing effects in the early 3 yr of this study were small and mixed, even though grazing intensities were moderate to high. For examples, there was some evidence of grazing-mediated reductions in both exotic and native species, with the canopy cover of native species increasing relative to exotic species from ungrazed to grazed treatments. Between 2007 and 2009, the ratios of native to exotic species canopy cover declined approximately 18% with grazing, and basal cover ratio declined 17%. Grazing had no significant effects on western wheatgrass, one of the most abundant native species on the site. Western wheatgrass is highly preferred by both small (Lauenroth and Milchunas 1992) and large (Milchunas et al. 2008) herbivores and generally declines with grazing in the native community (Milchunas et al. 1989). Grazing may have reduced canopy competition from weedy annual species enough to compensate for the negative effects of defoliation on this clonally expanding midheight species. Blue grama and buffalograss (*Buchloe dactyloides* [Nutt.] J. T. Columbus) would be favored by grazing (Milchunas et al. 1989) but have not yet been commonly established. Under the current species composition, grazing appears neutral to negative based on the response of these species groups. Because both western wheatgrass and the annual exotic cheatgrass are cool-season species but cheatgrass emerges and matures earlier in this location, a short window exists for opportunistic grazing timed to utilize cheatgrass. This opportunistic grazing appears to have some suppressive effect

on this undesirable exotic annual species. Long-term study of these treatments will be necessary to evaluate fully the more subtle, gradual effect of grazing compared with the immediate and dramatic effects of cover crop. These effects will need to be evaluated in conjunction with erosion, which was observed to be much greater on heavily than lightly grazed or ungrazed treatments during an exceptionally dry, windy winter.

Aboveground net primary production varied widely during the 3 yr of measurement but did not follow the usual linear pattern of increasing ANPP with increasing precipitation in grasslands due to drought periods followed by late-season rains in 2008. The consistently lower ANPP in native shortgrass steppe compared to the early seral CRP treatments may be explained by relatively greater belowground allocation in native perennial grass species compared to relatively greater aboveground allocation in annual forb species (Schenk and Jackson 2002; Milchunas et al. 2005c). Root biomass in native shortgrass steppe and the CRP treatments averaged 1 090 and 306 g · m⁻², respectively (Milchunas and Vandever, unpublished data), while ANPP averaged 126 and 321 g · m⁻²yr⁻¹ in the native shortgrass steppe and new CRP, respectively. With advances in successional development of the CRP field, we would expect greater root production and lower aboveground production, as allocation patterns switch from annual species that allocate primarily growth aboveground to native perennial species with intensive root systems (Schenk and Jackson 2002) that better control soil erosion and sequester greater amounts of carbon. Factors contributing to greater carbon input from roots compared to shoots include a high biomass turnover and exudation and sloughing (Milchunas 2009), lower tissue quality of roots (Milchunas et al. 2005a, 2005b), and ultraviolet radiation photo-oxidation (photodegradation) of aboveground exposed litter (Brandt et al. 2007) in this semiarid grassland.

Long-term heavy grazing of native shortgrass steppe can result in lower ANPP (Milchunas et al. 1994), but short-term grazing can result in compensatory regrowth and greater ANPP than ungrazed treatments (Milchunas et al. 2005a). We hypothesized this would not be the case for a community dominated by annual exotic weed species because grazing in native communities suppresses these species (Milchunas et al. 1992). Grazing increased ANPP in only the last of the 3 yr reported here, and additional years of study will be necessary to further evaluate this response. However, the lack of a negative effect of grazing on ANPP is noteworthy given the current policy of restricted grazing in CRP (US Department of Agriculture 2010). It was also unexpected that the allelopathic cover crop effect would still be evident six growing seasons after seeding. Plots previously planted to wheat tended to have greater ANPP than the plots previously planted to sorghum, probably because of the greater aboveground allocation of the weedy annual species that dominated the wheat plots compared with relatively greater belowground allocation of native perennial grass species on sorghum plots.

Mowing, like grazing, was of minor significance when compared with cover crop effects not only on annual weed species reduction but also on native perennial species establishment. Mowing is often the prescribed maintenance practice during the CRP establishment period because of its relatively low cost and high precision and is used to reduce competition

from annual weed species (Allen and Vandever 2003). Mowing was in some cases a less effective weed control practice than opportunistically timed selective grazing. However, litter cover on the mowed treatment was always greater than on grazed treatment. Litter remained in place better on the mowed than the ungrazed treatment, possibly because of wind loss from the ungrazed standing-dead canopy, except for after the exceptionally windy 2008–2009 winter, when litter accumulated on only the ungrazed treatment and was lost on the mowed. While removing portions of the canopy cover, grazing and mowing were not significant factors affecting total species vegetative basal cover after 3 yr of treatment in this community that was aggrading annually.

The differences between the sorghum and wheat cover crop treatments were dramatic and clearly evident (Figs. 1 and S1). We do not have proof of an allelopathic difference between sorghum and wheat under the field conditions during and after seeding of these CRP fields, but other causative factors may produce opposite results to those observed (see detailed discussion in Table S2, available at <http://dx.doi.org/10.2111/REM-D-10-00117.s2>). The effects of cover crop species and timing of planting and harvest on soil water, high nutrient and/or low carbon levels in soil, and abundance of arbuscular mycorrhizal fungi or other microbial associations other than those affected by allelopathy could possibly be alternative factors in the responses we observed. However, the timing of harvesting the two cover crops and autumn spraying of volunteer wheat and the dry autumn prior to seeding (see the “Methods” section) and other attributes of wheat versus sorghum in most cases argue against these other possibilities (Table S2), but the ability to prove allelopathy under field conditions can be difficult even in studies specifically designed to do so (Weidenhamer et al. 1989). Researchers and reviews in allelopathy often conclude that “full proof of allelopathy may never be attained” (Weidenhamer 1996) because allelopathy can directly or indirectly affect not only nutrient cycling and mycorrhizal fungi but also intraspecific competition and diversity (Langheim 1994) and herbivory by insects and livestock (Corcuera et al. 1992).

The very large effects of sorghum compared with wheat planted strips in this study indicate an important management option for improving native perennial species establishment on seeded CRP fields, abandoned cropland, and native revegetation projects. Because of the dry conditions in immediate years after seeding, the low establishment of perennial native grass species cover in the wheat strips by 2009 was below what may be considered a successful planting by US Natural Resource Conservation Service standards but was sufficient in the sorghum strips. The advantage gained by suppressing competition by weed species allowed for increasingly greater annual increases in the clonal, rhizomatous western wheatgrass from low initial densities in the sorghum strips to statistically and visually obvious differences by the last year of this study (Figs. 1 and S1).

Wheat can also be mildly allelopathic (Singh et al. 2003; Khanh et al. 2005; Belz 2007), but sorghum is reported to be a particularly allelopathic forage crop (Cheema et al. 2007). Because of sorghum’s allelopathic properties, some work has been conducted on differences in the allelopathic potential of cultivars (Czarnota et al. 2003; Singh et al. 2003). The effects

of an allelopathic species on desirable species can also vary. Given the large potential benefits reported here, additional research may be warranted specific to rangeland revegetation goals. This research could address three primary areas: 1) levels of allelopathy produced by different cover crop species and cultivars within a species (optimizing impacts), 2) variable resistances of seeded and desirable species for establishment (to better integrate site preparation management and seeding mixes), and 3) susceptibility of particular weed competitor and undesirable species to different allelochemicals in the cover crop species (to target particular pests). Cover crops can reduce soil erosion relative to fallowing but can also reduce soil moisture, and these types of trade-offs also need to be studied.

There are limitations of our study. We report on only one seeding in one particular year, which limits our ability to extrapolate to other fields and other environmental conditions. Conditions postseeding were dry and clearly reduced establishment compared with those observed in the past in other fields seeded during favorable wetter years. We do not know whether good conditions for germination may lessen or override cover crop effects we report here. Allelopathy can be density dependent with a higher abundance of plants “diluting” the allelochemicals and reducing toxicity, and wetter conditions can enhance breakdown of allelopathic compounds in the soil (Blair et al. 2006). Harsh conditions due to drought or soil type can potentially influence allelopathic effects (Weidenhamer et al. 1989; Langheim 1994). The large effects of the prior cover crop on establishment of seeded species in this study do, however, suggest a fruitful avenue of further research and suggest that allelopathic cover crops can be useful at least under dry conditions. Dry conditions for seeding establishment in arid and semiarid regions are common and probably the prevalent reason for slow development or the need to reseed. Herbicides and mowing are the commonly prescribed means of weed species control on newly seeded areas (e.g., see Yenish et al. 1998), which involve economic inputs that can be environmentally detrimental. Rangeland management and native plant community restoration may benefit from application of allelopathy research in cropping practices from sustainable agriculture and in how grazing further modifies subsequent exotic and native species dynamics.

IMPLICATIONS

In semiarid and arid regions, plant cover establishment is often primarily a function of unpredictable precipitation during the first few years after seeding and to a lesser degree seed mix and drilling methods. Practices promoting subsequent development generally revolve around mediating competition from weed species and can include high-energy input practices such as herbicides and mowing. Cover crops on fallow areas are often prescribed to control erosion prior to planting. Results from this study suggest that choice of cover crop species can be a significant management decision for the subsequent establishment and development of native perennial species vegetation. By examining alternative mechanisms for establishing robust deep-rooted long-term cover rather than more drought-susceptible cover dominated by annual plants, this study offers a potentially more effective practice for establishing deep-

rooted native vegetation to protect soils from erosion as well as increase root-carbon inputs to soil organic matter. Where and under what climatic and weather conditions allelopathic cover crops may be beneficial and which undesirable and desirable species may be sensitive and which may be resistant deserve more consideration by both land managers and researchers.

Opportunistic grazing can modify the effects of weather and cover crop on postestablishment dynamics of these early seral communities, and its use could be considered by policymakers and managers under limited intensities/timings for objective-driven management plans. The successful use of grazing to control exotic and invasive species may vary in particular locations with native plant species adaptations due to evolutionary history of grazing by native herbivores (Milchunas et al. 1988, 1992; Rinella and Hileman 2009) but has also been shown to be effective when applied in other systems in a controlled manner because modern plant communities can deviate from historical compositions and disturbance regimes (Davies et al. 2009; Firn et al. 2010). Lukin (1990) proposed succession management based on designed disturbance (grazing or mowing in the present study case), controlled colonization (cover crop species), and controlled species performances (rhizomatous species), and this framework has been modified by Krueger-Mangold et al. (2006) to include control of invasive species (exotic and annual species in the present study case). Grazing is currently authorized on CRP lands only outside the primary bird nesting season to provide emergency relief under drought conditions and for management of vegetation cover (restricted to no more than one in 5 yr in Colorado; US Department of Agriculture 2010). The minor effects of grazing in this study, when grazing intensities were both light and moderate to high, raise questions concerning the use of grazing to better manage vegetative establishment and weed species control given this policy.

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LITERATURE CITED

- ABHILASHA, D., N. QUINTANA, J. VIVANCO, AND J. JOSHI. 2008. Do allelopathic compounds in invasive *Solidago canadensis* s.l. restrain the native European flora? *Journal of Ecology* 96:993–1001.
- ALLEN, A. W., AND M. W. VANDEVER. 2003. A national survey of Conservation Reserve Program (CRP) participants on environmental effects, wildlife issues, and vegetation management on program lands. Fort Collins, CO, USA: US Geological Survey, Biological Science Report No. 2003-001. 51 p.
- BAINARD, L. D., P. D. BROWN, AND M. K. UPADHYAYA. 2009. Inhibitory effect of tall hedge mustard (*Sisymbrium loeselii*) allelochemicals on rangeland plants and arbuscular mycorrhizal fungi. *Weed Science* 57:386–393.

- BAUMHARDT, R. L., R. C. SCHWARTZ, L. W. GREENE, AND J. C. MACDONALD. 2009. Cattle gain and crop yield for a dryland wheat-sorghum-fallow rotation. *Agronomy Journal* 101:150–158.
- BELZ, R. G. 2007. Allelopathy in crop/weed interactions—an update. *Pest Management Science* 63:308–326.
- BLAIR, A. C., S. J. NISSEN, G. R. BRUNK, AND R. A. HUFBAUER. 2006. A lack of evidence for a role of the putative allelochemical (\pm)-catechin in spotted knapweed invasion success. *Journal of Chemical Ecology* 32:2327–2331.
- BRANDT, L. A., J. Y. KING, AND D. G. MILCHUNAS. 2007. Effects of altered ultraviolet radiation, litter chemistry, and precipitation on litter decomposition in shortgrass steppe. *Global Change Biology* 13:2193–2205.
- CALLAWAY, R. M., AND E. T. ASCHEHOUG. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523.
- CHEEMA, Z. A., AND A. KHALIQ. 2000. Use of sorghum allelopathic properties to control weeds in irrigated wheat in a semi arid region of Punjab. *Agriculture, Ecosystems, and Environment* 79:105–112.
- CHEEMA, Z. A., A. KHALIQ, M. ABBAS, AND M. FAROOQ. 2007. Allelopathic potential of sorghum (*Sorghum bicolor* L. Moench) cultivars for weed management. *Allelopathy Journal* 20:167–178.
- CHEEMA, Z. A., A. KHALIQ, AND S. SAEED. 2004. Weed control in maize (*Zea mays* L.) through sorghum allelopathy. *Journal of Sustainable Agriculture* 23:73–86.
- CORCUERA, L. J., V. H. ARGANDONA, AND G. E. ZÚNIGA. 1992. Allelochemicals in wheat and barley: role in plant-insect interactions. In: S. J. H. Rizvi and V. Rizvi [EDS.]. *Allelopathy, basic and applied aspects*. London, England: Chapman and Hall. p. 119–127.
- CZARNOTA, M. A., A. M. RIMANDO, AND L. A. WESTON. 2003. Evaluation of root exudates of seven sorghum accessions. *Journal of Chemical Ecology* 29:2073–2083.
- DAVIES, K. W., T. J. SVEJCAR, AND J. D. BATES. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications* 19:1536–1545.
- FIRN, J., A. P. N. HOUSE, AND Y. M. BUCKLEY. 2010. Alternative states models provide an effective framework for invasive species control and restoration of native communities. *Journal of Applied Ecology* 47:96–105.
- GILLEN, R. L., J. A. ECKROAT, AND F. T. MCCOLLUM III. 2000. Vegetation response to stocking rate in southern mixed-grass prairie. *Journal of Range Management* 53:471–478.
- GRMAN, E., AND K. N. SUDING. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology* 18:664–670.
- JACKSON, J. R., AND R. V. WILLEMSEN. 1976. Allelopathy in the first stages of succession on the Piedmont of New Jersey. *American Journal of Botany* 63:1015–1023.
- KHANH, T. D., M. I. CHUNG, T. D. XUAN, AND S. TAWATA. 2005. The exploitation of crop allelopathy in sustainable agricultural production. *Journal of Agronomy and Crop Science* 191:172–184.
- KRUEGER-MANGOLD, J. M., R. L. SHELLEY, AND T. J. SVEJCAR. 2006. Toward ecologically-based invasive plant management on rangeland. *Weed Science* 54:597–605.
- KRUSE, M., M. STRANDBERG, AND B. STRANDBERG. 2000. Ecological effects of allelopathic plants—a review. Silkeborg, Denmark: Ministry of Environment and Energy, National Environmental Research Institute Technical Report 315. 66 p.
- LABRADA, R. 2008. Allelopathy as a tool for weed management. *Allelopathy Journal* 22:283–288.
- LANGHEIM, J. H. 1994. Higher plants terpenoids: a phytocentric overview of their ecological roles. *Journal of Chemical Ecology* 20:1223–1279.
- LAUENROTH, W. K., AND D. G. MILCHUNAS. 1992. The shortgrass steppe. In: R. T. Coupland [ED.]. *Natural grasslands, introduction and western hemisphere*. Ecosystems of the World 8A. Amsterdam, Netherlands: Elsevier. p. 183–226.
- LIEBMAN, M., AND E. DYCK. 1993. Crop rotation and intercropping strategies for weed management. *Ecological Applications* 3:92–122.
- LUKEN, J. O. 1990. *Directing ecological succession*. New York, NY, USA: Chapman and Hall. 251 p.
- MILCHUNAS, D. G. 2009. Estimating root production: comparison of 11 methods in shortgrass steppe and review of biases. *Ecosystems* 12:1381–1402.
- MILCHUNAS, D. G., J. R. FORWOOD, AND W. K. LAUENROTH. 1994. Productivity of long-term grazing intensity treatments in response to seasonal precipitation. *Journal of Range Management* 47:133–139.
- MILCHUNAS, D. G., W. K. LAUENROTH, I. C. BURKE, AND J. K. DETLING. 2008. Effects of grazing on vegetation in the shortgrass steppe. In: W. K. Lauenroth and I. C. Burke [EDS.]. *Ecology of the shortgrass steppe: a long-term perspective*. New York, NY, USA: Oxford University Press. p. 389–446.
- MILCHUNAS, D. G., W. K. LAUENROTH, AND P. L. CHAPMAN. 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia* 92:520–531.
- MILCHUNAS, D. G., W. K. LAUENROTH, P. L. CHAPMAN, AND M. K. KAZEMPOUR. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11–23.
- MILCHUNAS, D. G., A. R. MOSIER, J. A. MORGAN, D. LECAIN, J. Y. KING, AND J. A. NELSON. 2005a. Elevated CO₂ and defoliation effects on a shortgrass steppe: forage quality versus quantity for ruminants. *Agriculture, Ecosystems, and Environment* 111:166–184.
- MILCHUNAS, D. G., A. R. MOSIER, J. A. MORGAN, D. LECAIN, J. Y. KING, AND J. A. NELSON. 2005b. Root production and tissue quality in a shortgrass steppe exposed to elevated CO₂: using a new ingrowth method. *Plant and Soil* 268:111–122.
- MILCHUNAS, D. G., O. E. SALA, AND W. K. LAUENROTH. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.
- MILCHUNAS, D. G., M. W. VANDEVER, F. KNOPF, AND A. W. ALLEN. 2005c. Refining Conservation Reserve Program management to meet regional objectives: evaluation of limited grazing on succession and stability of CRP grasslands in shortgrass steppe of eastern Colorado. In: A. W. Allen and M. W. Vandever [EDS.]. *The Conservation Reserve Program—planting for the future*. Proceedings of a National Symposium; 6–9 June 2004; Fort Collins, CO, USA. Fort Collins, CO, USA: US Geological Survey, Biological Resources Division, Scientific Investigations Report 2005-5145. p. 158–162.
- PERRY, L. G., S. A. CRONIN, AND M. W. PASCHKE. 2009. Native cover crops suppress exotic annuals and favor native perennials in a greenhouse competition experiment. *Plant Ecology* 204:247–259.
- PRATI, D., AND O. BOSSDORF. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *American Journal of Botany* 91:285–288.
- RICE, E. L. 1984. *Allelopathy*. Orlando, FL, USA: Academic Press. 422 p.
- RINELLA, M. J., AND B. J. HILEMAN. 2009. Efficacy of prescribed grazing depends on timing intensity and frequency. *Journal of Applied Ecology* 46:796–803.
- SCHENK, H. J., AND R. B. JACKSON. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90:480–494.
- SINGH, H. P., D. R. BATISH, AND R. K. KOHLI. 2003. Allelopathic interactions and allelochemicals: new possibilities for sustainable weed management. *Critical Reviews in Plant Sciences* 22:239–311.
- URBANO, B., F. GONZÁLEZ-ANDRÉS, AND A. BALLESTEROS. 2006. Allelopathic potential of cover crops to control weeds in barley. *Allelopathy Journal* 17:53–64.
- US DEPARTMENT OF AGRICULTURE. 2010. Conservation Reserve Program. <http://www.fsa.usda.gov/FSA/webapp?area=home&subject=copr&topic=crp-eg>. Accessed 19 January 2010.
- VERMEIRE, L. T., R. K. HEITSCHMIDT, AND M. R. HAERKAMP. 2008. Vegetation response to seven grazing treatments in the northern Great Plains. *Agriculture, Ecosystems, and Environment* 125:111–119.
- WEIDENHAMER, J. D. 1996. Distinguishing resource competition and chemical interference—overcoming the methodological impasse. *Agronomy Journal* 88:866–875.
- WEIDENHAMER, J. D., D. C. HARTNETT, AND J. T. ROMEO. 1989. Density dependent phytotoxicity: distinguishing resource competition and allelopathic interference in plants. *Journal of Applied Ecology* 26:613–624.
- YENISH, J., M. STANNARD, J. NELSON, AND G. MCKINNEY. 1998. Weed management for cover establishment and maintenance on Conservation Reserve Program acres. In: *Conservation Reserve Program technology*. Spokane, WA, USA: Natural Resources Conservation Service, Technical Notes, Plant Materials—15.