

# Controls of vegetation structure and net primary production in restored grasslands

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## Summary

1. Vegetation structure and net primary production (NPP) are fundamental properties of ecosystems. Understanding how restoration practices following disturbance interact with environmental factors to control these properties can provide insight on how ecosystems recover and guide management efforts.

2. We assessed the relative contribution of environmental and restoration factors in controlling vegetation structure, above- and below-ground investment in production across a chronosequence of semi-arid Conservation Reserve Program (CRP) fields recovering from dry land wheat cropping relative to undisturbed grassland. Importantly, we determined the role of plant diversity and how seeding either native or introduced perennial grasses influenced the recovery of vegetation properties.

3. Plant basal cover increased with field age and was highest in CRP fields seeded with native perennial grasses. In contrast, fields seeded with introduced perennial grasses had tall-growing plants with relatively low basal cover. These vegetation structural characteristics interacted with precipitation, but not soil characteristics, to influence above-ground NPP (ANPP). Fields enrolled in the CRP for > 7 years supported twice as much ANPP as undisturbed shortgrass steppe in the first wet year of the study, but all CRP fields converged on a common low amount of ANPP in the following dry year and invested less than half as much as the shortgrass steppe in below-ground biomass.

4. ANPP in CRP fields seeded with native perennial grasses for > 7 years was positively related to species richness, whereas ANPP in CRP fields seeded with introduced perennial grasses was controlled more by dominant species.

5. *Synthesis and applications.* Seeding with introduced, instead of native, perennial grasses had a strong direct influence on vegetation structure, including species richness, which indirectly affected NPP through time. However, the effects of restoring either native or introduced grasses on NPP were secondary to low water availability. Therefore, restoration strategies that maximize basal cover and below-ground biomass, which promote water acquisition, may lead to high resilience in semi-arid and arid regions.

**Key-words:** Conservation Reserve Program, diversity and ecosystem function, non-native species, net primary production, perennial grass, shortgrass steppe, species richness

## Introduction

A common goal of restoration in degraded landscapes is the recovery of vegetation structure and ecosystem function (Dobson, Bradshaw & Baker 1997). Restoration practices that promote perennial plant cover and diversity can have a strong bearing on the productivity and resilience of a plant community (Tilman *et al.* 1997; Pfisterer

& Schmid 2002). However, interactions among climate, soil and landscape properties can constrain the efficacy of restoration by influencing the rate or trajectory of recovery (Grman, Bassett & Brudvig 2013). As ecosystems come under increasing pressure from land-use intensification due to a growing human population, there is an imperative need to understand the degree to which restoration factors can influence the recovery of vegetation structure and productivity relative to the physical and biotic environment.

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Land conversion from native ecosystems to croplands has occurred on 27% of the global land surface and will likely intensify with an expanding demand for food and fibre (MEA 2005). Cropping is a novel disturbance that is not part of the evolutionary history of grasslands, which has led to large-scale declines in native plant cover and diversity (Fargione *et al.* 2008), soil mass through erosion, carbon storage, and nutrient availability (Burke *et al.* 1989), and loss of wildlife habitat and connectivity (Saunders, Hobbs & Margules 1991). There is further concern that cultivation contributes to greenhouse gases through accelerated decomposition and other pathways (Stocker *et al.* 2013). Cropping has been particularly pronounced across the Great Plains of the United States over the last 150 years (Lauenroth & Milchunas 1992). In the semi-arid western Great Plains, cropland is marginal due to low water availability that limits production and leaves soils exposed to erosion. In part due to these negative consequences, many incentive programs that began as early as the 1930s have encouraged farmers to take their land out of production and restore it to perennial vegetation (Dimitri, Efland & Conklin 2005). The Conservation Reserve Program (CRP) in the United States is similar to other agricultural incentive programs around the world in that it promotes maintaining a resource base for crop production (Scherr & McNeely 2008). CRP has paid farmers to convert cropland to perennial vegetation since 1985 and at its peak from 2002–2008 included almost 16 million hectares (USDA-FSA 2013). Immediately after enrolling a field in the CRP, farmers must plant it with perennial grasses using one of the approved seed mixes.

Time since CRP enrolment and seed mix are two important restoration factors that can influence vegetation structure and net primary production (NPP) of CRP grasslands. In eastern Colorado, where CRP is a major land use, the plant community composition transitions from early successional species to seeded perennial grasses as time since CRP enrolment increases (Munson & Lauenroth 2012). However, many of the seed mixtures contain perennial grasses not native to the shortgrass steppe, which can have a large influence on vegetation structure and ecosystem properties (Munson, Lauenroth & Burke 2012). Early successional and introduced (non-native) species are likely to alter plant basal cover, height and density in CRP fields, thereby affecting the capacity for NPP and its allocation above- versus below-ground, relative to fields seeded with native perennial grasses and undisturbed shortgrass steppe. Differences in species richness and composition among CRP fields may also influence NPP, providing insight on the role of diversity on ecosystem function (Tilman *et al.* 1997).

Vegetation structure and NPP are limited by water availability and soil properties. Low mean annual precipitation in the shortgrass steppe limits the species in the plant community, their respective structures and contribution to NPP in the long term (Lauenroth & Sala 1992). At a shorter timescale, high variability in annual

precipitation can result in fluctuations in vegetation structure and NPP determined by the growth responses of species in the field. Water availability is modified by soil texture. Coarse-textured soils in semi-arid regions support relatively high NPP compared to fine-textured soils due to high infiltration and reduced evaporative loss (Noy-Meir 1973). Soil nitrogen availability can also influence NPP but covaries with precipitation and is therefore difficult to determine how much it independently affects NPP (Burke, Lauenroth & Parton 1997). An assessment of the environmental factors over a gradient of CRP field ages and seed mixes through time can help elucidate how they interact to control vegetation structure and NPP.

Our objective was to answer the following questions: (i) How do restoration and environmental factors interact to affect vegetation structure and NPP in CRP fields through direct and indirect pathways? and (ii) How does vegetation structure and NPP in CRP fields compare to undisturbed shortgrass steppe? The restoration factors we examined include whether native or introduced perennial grass seed mixes were sown and the time since CRP enrolment, while the environmental factors we assessed were precipitation amount and seasonality, soil texture and nitrogen availability. We define vegetation structure to be both physical properties, including basal cover, height and density, in addition to the compositional property, species richness.

## Materials and methods

### STUDY SITES

We conducted this study at undisturbed shortgrass steppe sites within the Central Plains Experimental Range (CPER, Shortgrass Steppe Long-Term Ecological Research site) located 60 km north-east of Fort Collins, Colorado (40° 49' N, 107° 47' W), and Conservation Reserve Program (CRP) sites located within 13 km to the south and 3 km to the west of the CPER. The climate is semi-arid with a long-term mean annual precipitation (1969–2010) of 332 mm (SD = 99 mm), 80% of which falls between April and September, and a mean annual temperature of 9.6 °C (SD = 1.1 °C). Undisturbed shortgrass steppe is co-dominated by the C<sub>4</sub> perennial grasses *Bouteloua gracilis* and *Buchloe dactyloides* (plant nomenclature follows Great Plains Flora Association 1986). Other important functional types included C<sub>3</sub> graminoids, forbs, dwarf shrubs and prickly pear cactus. Our shortgrass steppe sites had been moderately grazed in the summer over the long term, but we excluded them from grazing during the study.

We partitioned CRP sites into those seeded with perennial grasses and forbs that occur in northern Colorado (native) and those seeded with perennial grasses that do not occur in northern Colorado (introduced). The native seed mix contained *Agropyron smithii* (~30% weight of all seed), *B. gracilis* (~20%), *Bouteloua curtipendula* (~20%), other perennial grasses (~20%) and *Dalea purpurea* (~10%). The introduced seed mix contained either *Agropyron intermedium* (100%) or *Bromus inermis* (100%), which are both perennial grasses from Europe and Asia. To address how time since CRP enrolment affected vegetation structure and NPP,

we established a chronosequence in only fields seeded with native perennial grasses, which consisted of three field age classes: early, mid and late. We sampled each field for 3 years to account for environmental variability. Early fields represented 2–4 years after CRP enrolment and were dominated by forbs and annual grasses (Munson & Lauenroth 2012), midfields represented 7–9 years after CRP enrolment and were composed of forbs and annual and perennial grasses, and late fields represented 18–20 years after CRP enrolment and were dominated by perennial grasses. To address how differences in seed mix affected vegetation structure and NPP, we controlled for field age and compared late CRP fields seeded with native perennial grasses to late CRP fields seeded with introduced perennial grasses over the course of the 3-year study.

All fields were in a non-irrigated wheat-fallow rotation prior to CRP enrolment. The year of CRP enrolment, fields were seeded with a sterile sorghum cover crop to protect the seedbed and discourage annual weed growth (NRCS 1991). A year later, fields were double-disked and drill-seeded with perennial grasses ( $\sim 0.5$  seed  $\text{g m}^{-2}$ ) to a 1.3 cm depth and 20-cm spacing between rows. Surface soil (0–5 cm) textures were loamy sand, sandy loam and sandy clay loam. All sites had similar topographic relief ( $< 3\%$  slope). We replicated each of the six field types three times for a total of eighteen fields sampled (6 field types  $\times$  3 field replicates = 18 fields sampled).

#### SAMPLING METHODS

We measured species richness, plant height, density and basal cover in forty 0.25-m<sup>2</sup> circular quadrats (spaced 20 m apart) in each CRP field and undisturbed shortgrass steppe from late August to early September in 2005, 2006 and 2007. We measured the maximum foliage height of a representative plant of each species and then calculated an average height of all species within a quadrat. Plant density was determined by counting the number of individual established plants within a quadrat, which did not include small seedlings. For clonal species, an individual plant was defined as a group of tillers connected by a crown (Coffin & Lauenroth 1988). Plant basal cover was assessed by assigning a cover value that represented the projected basal extent of all plant species within the quadrat. In each year of the study, we estimated above-ground net primary production (ANPP) by species in a subset of eight of the quadrats (spaced 40 m apart) used to sample vegetation structure. ANPP was estimated by clipping above-ground biomass at the soil surface, sorting out dead biomass from previous growing seasons and weighing after drying at 55 °C for 48 h. Because of the early senescence of *Bromus tectorum*, an introduced winter annual grass, we estimated its height, density, basal cover and ANPP in early June and incorporated these into the field estimates.

To determine below-ground biomass, we removed eight soil cores (5 cm in diameter and 30 cm in depth) in early May 2005 directly under the dominant perennial grass and eight cores from an adjacent grass interspace (10 cm away from the nearest plant) in each CRP field and undisturbed shortgrass steppe. This sampling stratification was done to encompass spatial variation in root biomass (Hook, Burke & Lauenroth 1994). Sampling was not stratified in early CRP fields because there were no perennial grasses. We subdivided the cores into 0–5-, 5–10-, 10–20- and 20–30-cm increments and oven-dried them at 55 °C to prevent decomposition. We used a 30-g subsample of soil from the cores

to determine soil texture by the hydrometer method (Day 1965). Roots were separated from soil cores at each depth increment using a hydropneumatic root elutriator (Smucker, McBurney & Srivastava 1982), oven-dried again at 55 °C and weighed.

We used ion exchange resin bags to estimate *in situ* inorganic soil N (Binkley & Matson 1983) adjacent to the NPP plots. We installed the bags 5 cm below the soil surface at each microsite (between,  $n = 8$ , and under,  $n = 8$ , perennial grasses) in early June and collected the bags in September in each year of the study. Inorganic N (nitrate and ammonium) was extracted from the bags using a KCl solution, and concentrations were colorimetrically determined with an Alpkem Flow Solution Autoanalyzer (Alpkem Corporation, Clackamas, OR, USA).

#### STATISTICAL ANALYSES

We performed analysis in two complementary stages. First, we determined how restoration factors directly affected vegetation structure and NPP relative to undisturbed shortgrass steppe. To do this, we performed repeated-measures analysis of variance to understand how time since CRP enrolment and seed mix affected vegetation structure and ANPP, as well as to compare these vegetation properties to undisturbed shortgrass steppe. Seed mix was the main effect, and year was the repeated measure modelled in an autoregressive correlation structure (Proc Mixed, SAS 9.2, SAS Institute Inc. 2002–2008, Cary, NC, USA). We used Tukey's multiple comparison adjustment when comparing field types separately for each year and years separately for each field type (Proc Glimmix, SAS 9.2). When there was a significant year effect, regression was performed to evaluate the rate of change of plant basal cover, height and density across CRP fields in the chronosequence (Proc Reg, SAS 9.2). Regressions were performed using vegetation structure from individual years, not age classes, to collectively account for successional change and interannual variability in all CRP fields in the chronosequence. Below-ground biomass was only measured in 2005. Therefore, analysis of variance was performed with field type and depth as main effects. We report below-ground biomass and inorganic soil N at the field scale by weighting measurements taken under and between plants according to the plant basal cover measurements taken in each field and the remaining bare ground not covered by plants, respectively (Vinton & Burke 1995).

Secondly, to better understand the relative contribution of direct effects of restoration factors, precipitation and soil properties on above-ground net primary production in CRP fields, and indirect effects through vegetation structural properties, we used structural equation modelling (SEM; Bollen 1989; Grace 2006). SEM estimates causal effects through path relations and examines both direct and indirect relationships between variables, thereby evaluating hypotheses about mediating factors. We developed an *a priori* model of our system, wherein seed mix, time since CRP enrolment, annual precipitation, soil texture and nitrogen availability influenced above-ground net primary production both directly and indirectly through plant density, basal cover, height and species richness. Log-transformations were performed on plant density, basal cover and height to correct for non-normality, and seed mix was entered into the model as a composite variable because it was a categorical predictor (Grace 2006). Model estimation was based on maximum likelihood, and model fit was evaluated using a chi-square test and the root mean square error of approximation (RMSEA) (AMOS 22.0.0, IBM SPSS 2013,

Meadville, PA, USA). Due to small sample size, we used additional estimation techniques that are sample size independent, including a Joreskog's goodness-of-fit index (GFI) and a bootstrapped Bollen–Stine test. The  $P$ -value in the chi-square and Bollen–Stine tests indicates the probability that a model fits the data, and unlike most tests, a high  $P$ -value indicates a better model. Other indications of good model fit are RMSEA  $<0.05$  and GFI  $>0.95$ . Path coefficients were also evaluated using  $z$ -tests (equivalent to  $t$ -tests).

## Results

Both interannual variability and intra-annual variability in precipitation were high during the study. Annual precipitation was 370 mm in 2005, 301 mm in 2006 and 409 mm in 2007. Early growing season (April–June) precipitation in 2005 was 42% above the long-term mean, and late growing season (July–September) precipitation was 57% below the mean. 2006 and 2007 showed the opposite patterns, with early growing season precipitation 62% and 42% below the mean and late growing season precipitation 16% and 81% above the mean, respectively.

### VEGETATION STRUCTURE

Plant basal cover increased by 0.9% per year along the chronosequence ( $r^2 = 0.85$ ,  $P < 0.0001$ ; Fig. 1a). Late CRP fields seeded with native perennial grasses had significantly higher basal cover than late CRP fields seeded with introduced perennial grasses for all years of the study except in 2006, when there was no difference between late fields seeded with native perennial grasses and *A. intermedium*. Undisturbed shortgrass steppe had 1.7–5.3 times more plant basal cover than CRP fields for all years of the study. There was low interannual variability in plant basal cover in all CRP fields and undisturbed shortgrass steppe.

There was no significant change in plant height along the CRP chronosequence (Fig. 1b). In 2005, the average plant heights in late CRP fields seeded with *B. inermis* and *A. intermedium* were 8.7 and 13 cm higher, respectively, than late CRP fields seeded with a native seed mix. Average plant height in undisturbed shortgrass steppe was significantly lower in all years than late CRP fields except in 2007 for late CRP fields seeded with *B. inermis*.

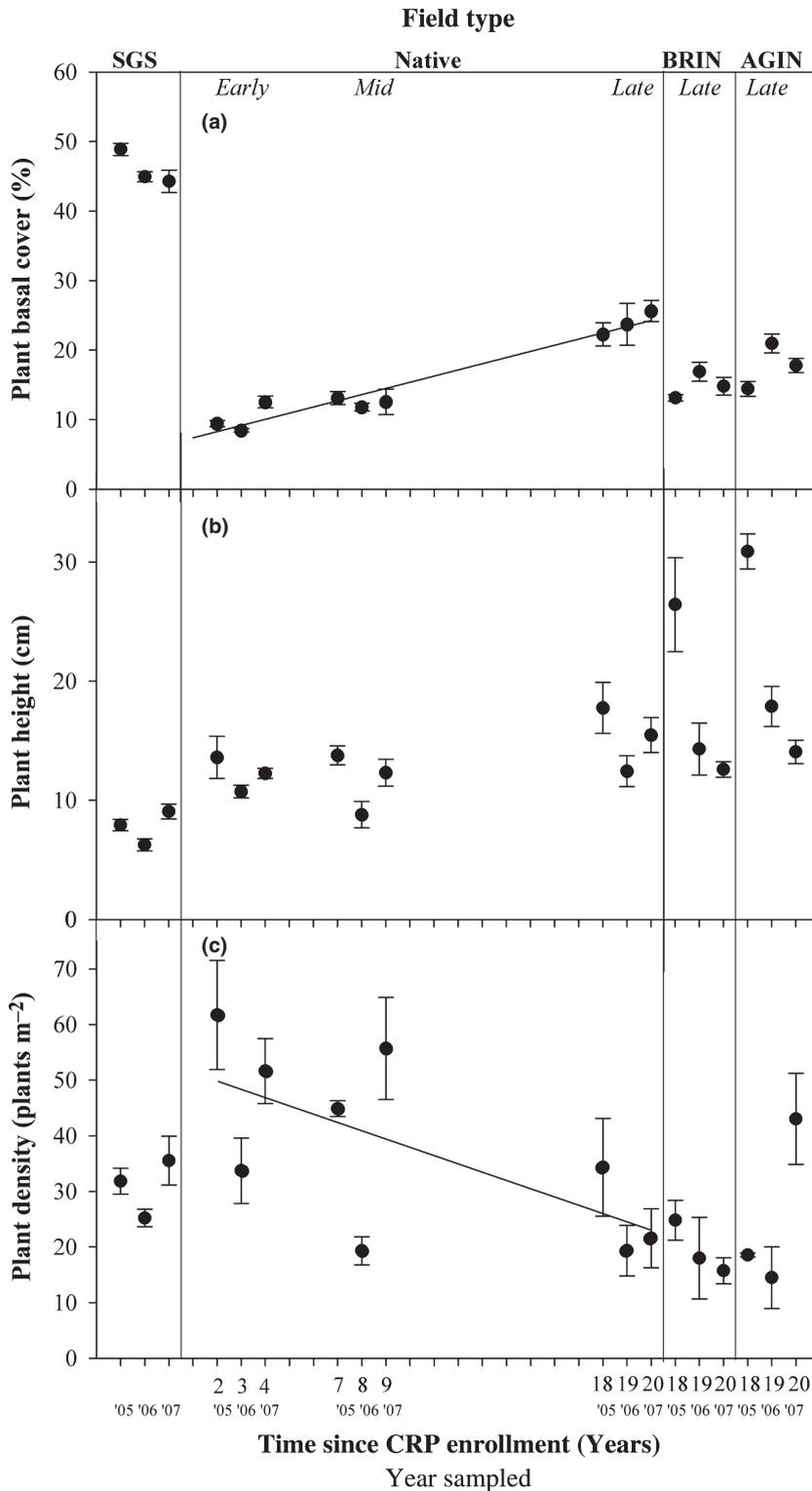
In contrast to basal cover, plant density decreased by 1.5 individuals per year over the chronosequence ( $r^2 = 0.31$ ,  $P < 0.05$ ; Fig. 1c). Plant density was not significantly different between late CRP fields seeded with native and introduced perennial grasses. Plant density in undisturbed shortgrass steppe was not significantly different from any late CRP fields in any years except in 2007, when it was higher than late CRP fields seeded with *B. inermis*. Interannual variability in plant density was high, especially in early and mid-CRP fields. Annual precipitation explained half the variability in these fields ( $r^2 = 0.49$ ,  $P = 0.001$ ).

### NET PRIMARY PRODUCTION

Above-ground net primary production (ANPP) increased from early-to-mid-CRP fields, where it reached its peak in 2007 (Fig. 2) and then decreased in late CRP fields. ANPP was greater in late CRP fields seeded with native compared to introduced perennial grasses in 2007, but there were no differences in 2005 and 2006. ANPP of introduced *B. inermis* and *A. intermedium* averaged 72% and 73% of the total ANPP in the fields in which they were, respectively, planted over the course of the study, whereas average ANPP of any one-seeded native perennial grass species did not exceed 20% of the field total. Mid- and late CRP fields had twice as much ANPP as undisturbed shortgrass steppe in 2005. Annual precipitation was a strong predictor of ANPP in CRP fields seeded with native perennial grasses ( $r^2 = 0.69$ ,  $P < 0.0001$ ) and a moderate predictor of ANPP in CRP fields seeded with introduced perennial grasses ( $r^2 = 0.28$ ,  $P = 0.03$ ), which was better explained by early growing season precipitation ( $r^2 = 0.71$ ,  $P < 0.0001$ ).

Below-ground biomass in the top 5 cm of soil was 75 g m<sup>-2</sup> in early CRP fields seeded with native perennial grasses and was significantly higher in mid- and late CRP fields seeded with native perennial grasses (Fig. 3). Below-ground biomass was lower in late CRP fields seeded with introduced perennial grasses than native perennial grasses, but these differences were not significant. Undisturbed shortgrass steppe had 2.0–3.6 times more below-ground biomass in the top 5 cm than CRP fields. There were no significant differences among CRP fields and between CRP fields and the shortgrass steppe in below-ground biomass at depths below 5 cm.

Our final structural equation model had satisfactory fit ( $\chi^2 = 5.98$ ,  $P = 0.82$ ,  $df = 13$ , GFI = 0.97, RMSEA = 0.01, Bollen–Stine  $P = 0.77$ ), but differed from our hypothesized model in that soil texture and nitrogen availability did not have significant explanatory power and the model fit improved when they were not included. Our model explained 26–78% of the variability in vegetation structural characteristics and 71% of the variability in above-ground net primary production (Fig. 4). Seed mix and time since CRP enrolment had moderate-to-strong effects (5 of 6 path coefficients:  $r \geq |0.50|$ ) on vegetation structural characteristics compared to weak direct effects on ANPP. The effect of precipitation ( $r = 0.58$ ) was twice as strong as seed mix ( $r = -0.31$ ) on ANPP, though structural characteristics influenced by restoration factors also had an effect on this ecosystem property ( $r = 0.27$ – $0.43$ ). Species richness had a positive effect on ANPP, which was largely attributable to mid- and late CRP fields seeded with native perennial grasses increasing 30 g m<sup>-2</sup> per additional species ( $r^2 = 0.48$ ,  $P < 0.01$ ; Fig. 5). In contrast, early CRP fields had lower-than-expected ANPP relative to high species richness, and late fields seeded with introduced perennial grasses generally had higher-than-expected ANPP relative to low species richness.

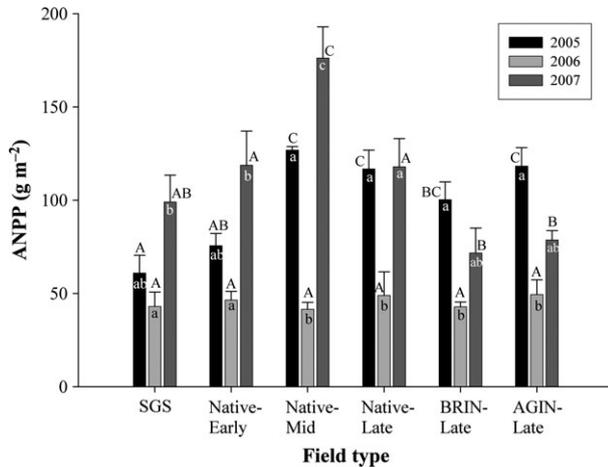


**Fig. 1.** Average plant basal cover (a), plant height (b) and plant density (c) ( $\pm$  SE) in undisturbed shortgrass steppe (SGS), early, mid- and late CRP fields seeded with native perennial grasses and late CRP fields seeded with introduced perennial grasses *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006 and 2007. Chronosequence linear regression:  $y = 0.89x + 6.6$ ,  $r^2 = 0.85$ ,  $P < 0.0001$  (basal cover),  $y = -1.5x + 53$ ,  $r^2 = 0.31$ ,  $P < 0.05$  (plant density).

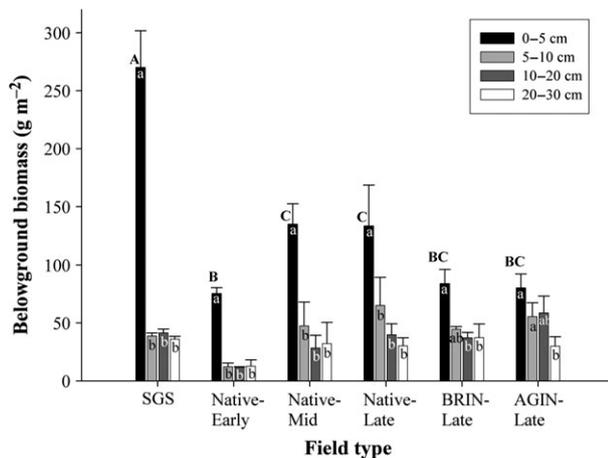
**Discussion**

The goal of many restoration projects is to re-establish perennial vegetation, but a complete understanding of the recovery of the ecosystem and its ability to be self-supporting and resilient to natural environmental variability requires an assessment of how restoration practices

interact with precipitation and soil properties to influence vegetation structure and productivity (SER 2004; Ruiz-Jaen & Aide 2005). We found that time since CRP enrollment and whether the perennial grasses in the restoration seed mix were introduced or native had strong direct effects on vegetation structure. However, the indirect effects of these restoration factors on NPP were secondary



**Fig. 2.** Above-ground net primary production (ANPP  $\text{g m}^{-2}$ ;  $\pm$ SE) in undisturbed shortgrass steppe (SGS), early, mid- and late CRP fields seeded with native perennial grasses and late CRP fields seeded with introduced perennial grasses *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006 and 2007. Different upper-case letters designate significant differences (Tukey adjusted  $P < 0.05$ ) in ANPP among field types within the same sampling year, and different lower-case letters designate significant differences (Tukey adjusted  $P < 0.05$ ) in ANPP among years within the same field type.



**Fig. 3.** Below-ground biomass ( $\text{g m}^{-2}$ ;  $\pm$  SE) at 0–5, 5–10, 10–20 and 20–30 cm depths in undisturbed shortgrass steppe (SGS), early, mid- and late CRP fields seeded with native perennial grasses and late CRP fields seeded with introduced perennial grasses *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005. Different upper-case letters designate significant differences (Tukey adjusted  $P < 0.05$ ) in below-ground biomass at 0–5 cm depth among field types. There were no significant differences in below-ground biomass at all other depth increments among field types. Different lower-case letters designate significant differences (Tukey adjusted  $P < 0.05$ ) in below-ground biomass among depth increments within the same field type.

to seasonal and annual precipitation below the mean. Plant species diversity influenced NPP in CRP fields >7 years old seeded with native perennial grasses, but not in younger CRP fields and fields seeded with introduced perennial grasses. All CRP fields had high above- relative

to below-ground investment in production relative to undisturbed shortgrass steppe. This allocation strategy may negatively influence the resilience of CRP fields to drought and grazing, conditions to which the shortgrass steppe is well adapted (Milchunas, Sala & Lauenroth 1988).

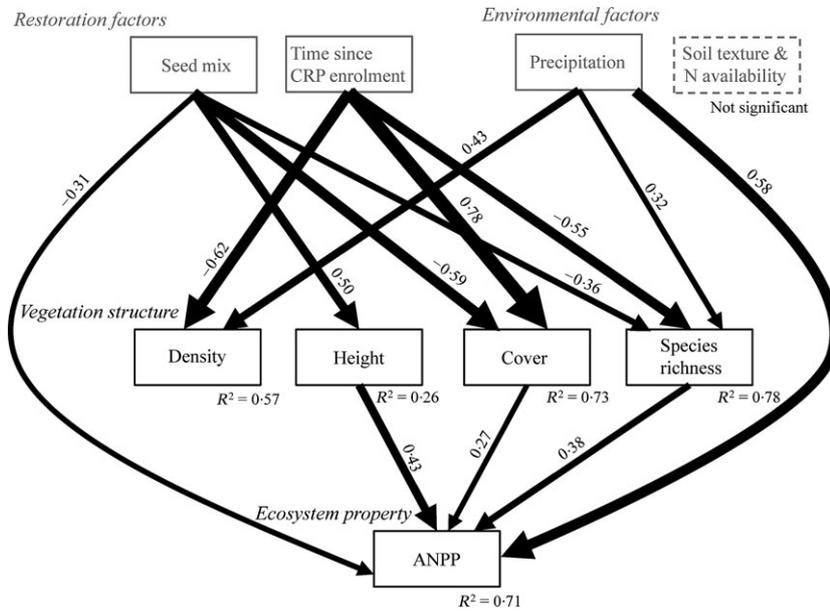
#### VEGETATION STRUCTURE

Time since CRP enrolment had a strong influence on vegetation structure. Plant basal cover increased 0.9% per year as perennial grasses established along the chronosequence, which is low compared to grassland recovery rates in mesic regions (Baer *et al.* 2002) but typical of rates in the drier shortgrass steppe (Coffin, Lauenroth & Burke 1996; Munson & Lauenroth 2009). Intense competition by perennial grass roots for limited soil water (Aguilera & Lauenroth 1993) most likely drove the decline in the abundance of annual species, which is partially supported by differences in plant density among CRP fields only occurring in years when annual precipitation was above the mean. Despite perennial grass establishment, full recovery of plant basal cover was not possible in twenty years under current CRP practices. Late CRP fields seeded with native perennial grasses reached half the basal cover of undisturbed shortgrass steppe and introduced perennial grasses recovered even less. As basal cover was slow to change in CRP fields, it was not surprising that this structural characteristic was unresponsive to interannual variability in precipitation. Lane, Coffin & Lauenroth (1998) found that basal cover was not related to annual precipitation across a gradient from shortgrass steppe to tallgrass prairie and it is likely more limited by long-term mean annual precipitation at a site.

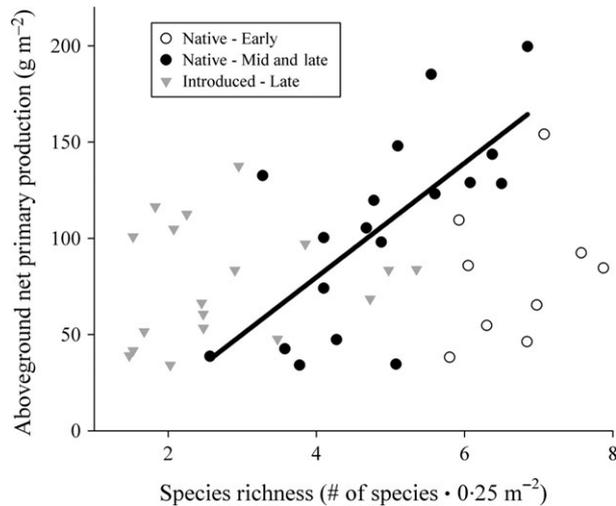
Seed mix, but not time since CRP enrolment, explained variance in average plant height because of the dominance of tall-growing introduced (> 60 cm) relative to native (< 40 cm) perennial grasses in the late CRP fields in which they were seeded. The structural difference between field types was not sustained after two consecutive dry early growing seasons, which reduced the average plant height in late CRP fields seeded with introduced perennial grasses by half. This sharp decrease coupled with the short stature of undisturbed shortgrass steppe suggests that low water availability may limit the height of perennial grasses that can be supported over the long term in this region. Fields seeded with introduced compared to native perennial grasses had low species richness (Munson & Lauenroth 2012), which indicates a negative consequence of promoting species that are non-native and the importance of restoration treatment on species diversity (Grman, Bassett & Brudvig 2013).

#### NET PRIMARY PRODUCTION

Annual precipitation is strongly related to ANPP in the native shortgrass steppe (Lauenroth & Sala 1992) and



**Fig. 4.** Final structural equation model ( $\chi^2 = 5.98$ ,  $P = 0.82$ ,  $df = 13$ ,  $GFI = 0.97$ ,  $RMSEA = 0.01$ , Bollen–Stine  $P = 0.77$ ) of the relative control of restoration (seed mix, time since CRP enrolment) and environmental factors (precipitation, soil texture and nitrogen availability) on vegetation structure and an ecosystem property in all CRP fields. Measured variables are in rectangles, causal relationships are indicated by arrows, and path coefficients (equivalent to correlation coefficients) are indicated by value next to the arrow and the width of the arrow. Explanatory power ( $R^2$ ) indicated for vegetation structural characteristics and above-ground net primary production. Only significant causal relationships and path coefficients are shown.



**Fig. 5.** Above-ground net primary production (ANPP g m<sup>-2</sup>) in early, mid- and late CRP fields seeded with native perennial grasses and late CRP fields seeded with introduced perennial grasses relative to species richness (# of species · 0.25 m<sup>-2</sup>). Native – mid- and late- linear regression:  $y = 29.7x - 39.0$ ,  $r^2 = 0.48$ ,  $P < 0.01$ .

adjoining cropland (Lauenroth, Burke & Paruelo 2000). Our results suggest that annual precipitation is the strongest driver of ANPP in a transition between these two land-cover types, and restoration factors influenced this ecosystem property indirectly through mediation of vegetation structure. CRP fields had high variability in ANPP because all fields > 7 years old supported twice as much ANPP as undisturbed shortgrass steppe in 2005, which was a year with above mean annual precipitation. In 2006, when annual precipitation was below the mean, there was no difference in ANPP between the shortgrass steppe and CRP fields and among CRP field types. This is consistent with the convergence of ANPP per unit precipitation in dry years across plant communities that

have different vegetation structures (Huxman *et al.* 2004). Mid-CRP fields had the strongest response of ANPP to precipitation due to the presence of the annual grass, *B. tectorum*, which is sensitive to changes in water availability (Bradford & Lauenroth 2006). Although annual precipitation influenced ANPP of CRP fields seeded with native C<sub>4</sub> perennial grasses, early growing season precipitation was a better predictor of ANPP in fields seeded with introduced C<sub>3</sub> perennial grasses. This relationship is similar to the northern mixed-grass prairie where there are more C<sub>3</sub>, early growing perennial grasses represented in the plant community. Low precipitation early and high precipitation late in the 2007 growing season explain why ANPP was lower in late fields with introduced perennial grasses and demonstrate the importance of precipitation timing to the outcome of revegetation efforts in this region (Milchunas & Vandever 2014). An unexpected result was that soil texture or nitrogen availability did not interact with water availability to influence ANPP in CRP fields given their importance in undisturbed shortgrass steppe (Lauenroth & Milchunas 1992).

When all CRP field types were considered, vegetation structure constrained ANPP (Lauenroth & Sala 1992), but only when annual precipitation was above average. Plant height and basal cover were significant predictors of ANPP because perennial grasses that contributed a large amount to production in CRP fields had relatively high basal cover (native perennial grasses) or grew to a tall height in a wet year (introduced perennial grasses). These structural characteristics likely affect net primary production through their influence on the number of meristems where plant growth occurs (Yahdjian & Sala 2006). Associated with reductions in plant height, CRP fields with introduced perennial grasses were negatively affected by drought, providing further support that they may not be well suited for a semi-arid climate.

The positive effect of species richness on ANPP in mid- and late CRP fields seeded with native perennial grasses provides some support of a coupling of diversity with ecosystem function (Tilman *et al.* 1997). This relationship may be attributable to a greater breadth of functional diversity in these fields in terms of photosynthetic pathway, longevity and growth form, which allowed plants to fill complementary niche space. For example, annual and perennial forbs and grasses co-occurred in relatively high abundance in mid-CRP fields, and C<sub>4</sub> and C<sub>3</sub> caespitose and rhizomatous grasses composed late CRP fields with relatively high species evenness (Munson & Lauenroth 2012). In contrast, ANPP in early CRP fields was dominated almost entirely by annuals, and ANPP in late CRP fields seeded with introduced perennial grasses was in most cases dominated by one perennial grass species. A previous study with similar species demonstrated that increasing the number of native, but not introduced, perennial grasses resulted in higher ANPP, which was attributable to differences in complementarity effects between species of different origins (Isbell & Wilsey 2011). Despite the relationship between plant species richness and ANPP in mid- and late CRP fields seeded with perennial grasses, there was a remarkably similar decline of ANPP in all CRP fields in 2006, when growing season precipitation was low. CRP fields and undisturbed shortgrass steppe with high species richness were not buffered against the decline through redundancy of functional types and compensation among species (Tilman *et al.* 1997; Pfisterer & Schmid 2002).

In contrast to high ANPP, below-ground biomass in CRP fields was significantly lower than undisturbed shortgrass steppe. This suggests that perennial grasses in CRP fields have not had the time to develop the extensive root system of undisturbed shortgrass steppe (Sims & Singh 1978). Although below-ground biomass increased from early-to-mid- and late CRP fields due to the establishment of perennial grasses, root growth in CRP fields may be limited by low plant basal cover. Low investment of below- relative to above-ground tissue indicates the potential for limited capacity to take up water and high transpiration water losses. The implications for this allocation of production may be susceptible to drought or grazing over the long term, which are strong selective forces in the shortgrass steppe (Milchunas, Sala & Lauenroth 1988). Despite no significant differences in below-ground biomass between late CRP fields seeded with native and introduced perennial grasses at the field scale, there was significantly higher biomass under native perennial grasses at the plant scale ( $t = 3.2$ ,  $P < 0.05$ ), which can create a higher input of carbon and nitrogen into soils over the long term (Munson, Lauenroth & Burke 2012).

#### CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The state and rate of recovery of vegetation structure and NPP following large-scale disturbances are critical to land

management in regions where low water availability interacts with restoration treatments to influence the establishment of perennial vegetation. Seeding practices led to a slow increase of plant basal cover and below-ground biomass, which were significantly lower than undisturbed shortgrass steppe after twenty years, while plant height and ANPP in recovering fields were significantly higher within 7 years of seeding than undisturbed shortgrass steppe. Many of these differences between recovering fields and undisturbed shortgrass steppe were more pronounced if fields were seeded with introduced compared to native perennial grasses. While management goals of reduced soil erosion and establishment of wildlife habitat may be met within a 10-year window of restoration (USDA-FSA 2013), plant survival in regions limited by water availability is dependent on a large investment in below-ground biomass (Burke *et al.* 1998). This structural advantage is reinforced because drought conditions reduced ANPP to the same level across all recovering fields and led to a sustained suppression of ANPP of the tall-growing introduced perennial grasses into the second year of low early growing season precipitation. We suggest that restoration practices that maximize below- relative to above-ground net primary production can increase water extraction and the resilience of perennial vegetation over the long term in dry land regions. Management practices that promote the establishment of native grasses adapted to drought, combined with suppression of annual species, may help facilitate this allocation of production. These practices include conducting restoration treatments in wet years, seeding locally sourced plant materials to the proper depth, the use of cover crops and implementing opportunistic grazing (NRCS 1991; Milchunas *et al.* 2011; Milchunas & Vandever 2014).

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