DISSERTATION

PLANT COMMUNITY AND ECOSYSTEM CHANGE ON CONSERVATION RESERVE PROGRAM LANDS IN NORTHEASTERN COLORADO

Submitted by

Seth M. Munson

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SETH M. MUNSON ENTITLED "PLANT COMMUNITY AND ECOSYSTEM CHANGE ON CONSERVATION RESERVE PROGRAM LANDS IN NORTHEASTERN COLORADO" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate work

[redacted]

[redacted]

[redacted]

[redacted]

Advisor

[redacted]

Department Head/Director

ABSTRACT OF DISSERTATION

PLANT COMMUNITY AND ECOSYSTEM CHANGE ON CONSERVATION RESERVE PROGRAM LANDS IN NORTHEASTERN COLORADO

The Conservation Reserve Program (CRP) is an important transitional land use that converts formerly cultivated land to perennial vegetation across the U.S. In the shortgrass steppe region of eastern Colorado, CRP currently includes nearly 1 million hectares of land seeded with native and introduced perennial grasses. Establishment of perennial grasses encourages the recovery of plant community and ecosystem properties altered by tillage and crop production practices. The objective of my dissertation was to determine how time since CRP enrollment, seed mix, and environmental variability affect plant community composition, vegetation structure, net primary production, and soil carbon and nitrogen relative to undisturbed shortgrass steppe.

As time since CRP enrollment increased, CRP fields transitioned from a species rich annual forb and grass community to a perennial grass dominated community with low species richness. Seed mix determined which perennial grasses increased in dominance, but slow and variable recovery allowed for a dynamic plant community composed of species with different life forms, photosynthetic pathways, and origins. Patterns of precipitation and interactions among species affected the relative differences in canopy cover between functional types.

Vegetation structure was indirectly influenced by time since CRP enrollment and seed mix through plant community composition. There was an increase in plant basal cover and height, and decrease in plant density as perennial grasses replaced annual grasses and forbs. These structural attributes constrained aboveground net primary production (ANPP), but only when water was not limiting. CRP fields had the potential to support twice as much ANPP as undisturbed shortgrass steppe in years above mean annual precipitation. However, belowground biomass and belowground net primary production (BNPP) were significantly lower in CRP fields than undisturbed shortgrass steppe, which has implications for their long-term survival in a water limited region.

Soil organic carbon was correlated to carbon input through BNPP from perennial grasses and increased at the plant scale as time since CRP enrollment increased. At the field scale, the carbon storage resulting from this increase was low in CRP fields compared to undisturbed shortgrass steppe. Nitrogen was closely linked to carbon in plants and soil and its availability was correlated to soil organic nitrogen, quantity and quality of belowground inputs, and precipitation.

Seth M. Munson
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Spring 2009

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Chapter 1: Introduction

The patchwork of land uses in the shortgrass steppe region of Colorado includes nearly 1 million hectares of land producing wheat each year (USDA National Agricultural Statistics Service 2008). Since this region is semiarid with marginal land for cropping, wheat is grown in rotation with a year-long fallow period to store soil water (Hart 2008). Dryland wheat-fallow cropping is unlike other disturbances, to which shortgrass steppe species have adapted (Milchunas et al. 1988), with long-term ecological consequences. Above and belowground components of a diverse plant community are destroyed and replaced with an annually harvested crop, which reduces the recovery potential of shortgrass steppe species (Coffin et al. 1996). Low plant inputs coupled with increased soil erosion and decomposition through tillage practices have led to losses in soil organic carbon and nutrient availability (Burke et al. 1995).

These changes in plant community composition and ecosystem properties can be reversed following the cessation of cropping practices. Early research described slow and variable plant community succession after the abandonment of cultivated fields in the shortgrass steppe region (Shantz 1917, Savage and Runyon 1937, Judd and Jackson 1939, Costello 1944). Constraints on water availability and the reproductive potential of shortgrass species can explain this recovery pattern (Hyder et al. 1971, Samuel 1985, Coffin and Lauenroth 1992). Despite short-term dominance of different functional types following disturbance, shortgrass species come to dominate the plant community in the long-term (> 50 years; Coffin et al. 1996). Ecosystem properties also change over the course of succession (Odum 1969).

Plant functional types and species differ in their structure and allocation of production, which can influence soil properties in the shortgrass steppe (Vinton and Burke 1995). Some fractions of SOC and nutrient availability can recover within 50 years of cropping cessation and are dependent on the establishment of perennial grasses (Burke et al. 1995).

Although changes in plant community and ecosystem properties occur through succession following the cessation of cropping practices, human activity can modify the trajectory of recovery. Since 1985, the federal government has paid farmers to take their land out of production and seed their fields with perennial vegetation through the Conservation Reserve Program (CRP). CRP is an extensive land use nationwide and in Colorado currently includes an area equivalent to the land producing wheat (USDA Farm Service Agency 2008). CRP fields in the shortgrass steppe region are seeded with a variety of seed mixes that contain perennial grasses to reduce soil erosion through the establishment of plant cover (Skold 1989).

There are few studies which examine plant community and ecosystem change on CRP land. The research that does exist is largely descriptive of plant community and vegetation structure associated with suitable avian habitat (Burger et al. 1990, Millenbah 1996, McCoy et al. 2001). Other studies are not specific to CRP land use, but address plant community and ecosystem change following the conversion from cropping to perennial grassland (i.e. Paschke et al. 2000, Brown and Bugg 2001, Camill et al. 2004, Zeiter et al. 2006, Foster et al. 2007). Results from this body of research can provide insight about recovery in CRP fields. Baer et al. (2002) examined CRP plant community and ecosystem changes in the tall grass prairie region, where precipitation is higher than shortgrass steppe. A comparison of my results to this study can lead to an understanding of how precipitation drives recovery patterns in CRP fields.

Research that addresses changes in soil carbon and nitrogen in CRP fields is more common (Gebhart et al. 1994, Follett et al. 2001, Kucharik et al. 2003) and suggests variable recovery rates. Two studies specific to the shortgrass steppe (Robles and Burke 1997 and 1998, Reeder et al. 1998) determined that recovery is slow in the first ten years of CRP enrollment. My study expands on these studies because it examines two decades of recovery following reenrollment in CRP and addresses the effect of using different seed mixes.

CRP fields can be used to test the rate of development and the duration of persistence of species and functional types that occur in succession using models developed in the shortgrass steppe (Judd and Jackson 1939, Costello 1944, Coffin et al. 1996). Early (recently enrolled) CRP fields are likely influenced by the seed bank, dispersal and vegetative spread from neighboring fields. Low precipitation and high potential evapotranspiration in the shortgrass steppe region (Lauenroth and Bradford 2006) can limit plant establishment and growth, as well as the rate of succession through their influence on soil moisture. However, short-term wet-dry cycles drive fluctuations in species composition, especially in highly perturbed areas (Milchunas et al. 1990). Interactions among species and species modification of their environment can further contribute to changes in plant community composition during succession (Connell and Slatyer 1977). The plant community in late (older) CRP fields is more likely determined by species that established from the CRP seed mix. Since allowable seed mixes contain both native and introduced species (not native to northeastern Colorado), CRP fields can have a plant community that is compositionally similar or very different from undisturbed shortgrass steppe. Late CRP fields may also be influenced by colonizing perennial grasses, which compete with seeded perennial grasses.

Time since CRP enrollment and seed mix can indirectly affect vegetation structure and net primary production (NPP) through plant community composition. The species that establish in CRP fields may have a different growth form and allocation strategy than undisturbed shortgrass steppe. *Bouteloua gracilis*, the dominant perennial bunchgrass in the shortgrass steppe, has a relatively low above- to belowground NPP ratio (Milchunas and Lauenroth 2001), which makes it resistant to grazing and drought. In contrast, CRP fields may have more annual species that can grow at high density and allocate more NPP above- than belowground (Lauenroth et al. 1978). Many of the perennial grass species in the CRP seed mix are native to regions with greater water availability, where light is a more limiting factor in plant growth (Lauenroth and Coffin 1992). These species may also allocate more to aboveground NPP, but may have to compensate in a low water environment by having lower density and/or basal cover compared to undisturbed shortgrass steppe or restrict growth to years with high water availability. Potential differences in vegetation structure, such as height and basal cover, between fields seeded with mostly native and introduced perennial grasses may lead to differences in NPP (Lieth and Whittaker 1975, Lauenroth and Sala 1992).

CRP fields can store anthropogenic sources of carbon (C) from the atmosphere through the recovery of soil organic carbon (SOC; Burke et al. 1995, Conant et al. 2001) lost during wheat cropping. SOC is the largest terrestrial pool of organic C (Schimel 1995) and has a long residence time (Oades 1988), making it an important reservoir for C storage. Much effort has been made to elucidate global controls regulating inputs and outputs of SOC using meta-analysis (Post et al. 1982, Post and Kwon 2000) and modeling (Parton et al. 1987) approaches, while less effort has been made to link SOC to exchanges with the vegetation and atmosphere using an empirical approach. The size and dynamics of SOC in CRP fields are influenced by the quantity and quality of plant inputs, which may change with time since CRP enrollment and seed mix. Outputs from SOC, including soil respiration may also vary with time since CRP enrollment and seed mix due to changes in the plant and microbial community, soil resources and physical characteristics. Since C uptake and storage is tightly linked to the nitrogen (N) cycle (Vitousek and Howarth 1991, Diaz et al. 1993), it is equally important to understand how N pools and fluxes may be affected in CRP fields.

The overall objective of my dissertation is to determine how time since CRP enrollment, seed mix, and environmental variability affect the following variables in CRP fields relative to the shortgrass steppe:

1. Plant community composition
2. Vegetation structure and net primary production
3. Soil carbon and nitrogen

To accomplish my objective, I selected CRP fields in the West Greeley Conservation District, near the Central Plains Experimental Range (CPER, Shortgrass Steppe Long Term Ecological Research site) located 60 km northeast of Fort Collins, Colorado (40° 49' N, 107° 47' W). I used uncultivated shortgrass steppe sites on the CPER to compare to CRP fields. CRP fields were divided into those seeded with native and introduced perennial grasses. To address time since CRP enrollment, I established a chronosequence (Stevens and Walker 1970) that consisted of three field age classes: early (2 years after CRP enrollment), mid (7 years), and late (18 years). I only included fields seeded with a native seed mix in the chronosequence to minimize differences in the potential vegetation. To address seed mix, I controlled for field age and compared late CRP fields seeded with native perennial grasses to late CRP fields seeded with introduced perennial grasses. I measured and estimated plant community composition and a suite of ecosystem properties for 3 years (2005-2007) in each field to account for the effect of environmental variability, particularly precipitation.

The dissertation chapters are divided according to the variables outlined in my objective. Chapter 2 focuses on plant community composition, including plant species, functional type, and community-level patterns in CRP fields; Chapter 3 focuses on vegetation structure and net primary production in CRP fields; and Chapter 4 focuses on soil carbon and nitrogen in CRP fields. Chapter 5 summarizes my findings and presents the conclusions from my dissertation.

Literature Cited

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12: 1688-1701.

Brown, C.S., and R.L. Bugg. 2001. Effects of established perennial grasses on introduction of native forbs in California. Restoration Ecology 9: 38-48.

Burger, L.W., Jr. E.W. Kurzejeski, T.V. Dailey, and M.R. Ryan. 1990. Structural characteristics of vegetation in CRP fields in northern Missouri and their suitability as bobwhite habitat. Transactions of the North American Wildlife and Natural Resources Conference 55: 74-83.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program. Ecological Applications 5: 793–801.

Camill, P., M.J. McKone, S.T. Sturges, W.J. Severud, E. Ellis, J. Limmer, C.B. Martin, R.T. Navartil, A.J. Purdie, B.S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14: 1680-1694.

Coffin, D.P., and W.K. Lauenroth. 1992. Spatial variability in seed production of the perennial bunchgrass *Bouteloua gracilis* (Gramineae). American Journal of Botany 79: 347-353.

Coffin, D. P., W. K. Lauenroth, and I. C. Burke. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications 6: 538–555.

Conant, R.T., K. Paustian, and E.T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11: 343-355.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Costello, D.F. 1944. Natural revegetation of abandoned plowed land in the mixed grass prairie association of northeastern Colorado. Ecology 25: 312-326.

Diaz, S., J.P. Grime, J. Harris, and E. McPherson. 1993. Evidence of a feedback mechanism limiting plant response to elevated CO_2. Nature 364: 616-617.

Follett, R.F., S.E. Samson-Liebig, J.M. Kimble, E.G. Preussner, and S.W. Waltman.

2001. Carbon sequestration under the CRP in the historic grassland soils of the USA. Pages 27-49 *in* R. Lal and K. McSweeney, eds. Soil management for enhancing carbon sequestration, Special Publication 57 ed. Soil Science Society of America, Madison,Wisconsin.

Foster, B.L., C.A. Murphy, K. Keller, T. Aschenbach, E.J. Questad, and K. Kindscher. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. Restoration Ecology 15: 652-661.

Gebhart, D.L., H.B. Johnson, H.S. Mayeux, and H.W. Polley. 1994.The CRP Increases in soil organic carbon. Journal of Soil and Water Conservation 49: 488-492.

Hart, R.H. 2008. Land-use history on the shortgrass steppe. Pages 55-69 *in* W.K. Lauenroth and I.C. Burke, eds. Ecology of the shortgrass steppe. Oxford University Press, New York.

Hyder, D.N., Everson, A.C. and Bement, R.E. 1971. Seedling morphology and seeding failures with blue grama. Journal of Range Management 24: 287-292.

Judd, I.B., and M.L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. American Society of Agronomy Journal 39: 541-547.

Kucharik, C.J., J.A. Roth, and R.T. Nabielski. 2003. Statistical assessment of a paired-site approach for verification of carbon and nitrogen sequestration on Wisconsin Conservation Reserve Program land. Journal of Soil and Water Conservation 58: 58-67.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36: 211-222.

Lauenroth, W.K., and D.P. Coffin. 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. Pages 131-150 *in* Wali, M.K., ed. Ecosystem rehabilitation: preamble to sustainable development. Volume 2: Ecosystem analysis and synthesis. SPB Academic Publishing, The Netherlands.

Lauenroth, W.K., and O.E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2: 397-403.

Lauenroth, W. K., and J.B. Bradford. 2006. Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. Ecosystems 9:1-15.

Lieth, H., and R.H. Whittaker, eds. 1975. Primary productivity of the biosphere.

Ecological Studies, v. 14. Springer-Verlag, New York.

McCoy, T.D., E.W. Kurzejeski, L.W. Burger Jr., M.R. Ryan. 2001. Effects of Conservation practice, mowing, and temporal changes on vegetation on CRP fields in northern Missouri. Wildlife Society Bulletin 29: 979-987.

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.

Millenbah, K.F., S.R. Winterstein, H. Campa III, L.T. Furrow, and R.B. Minnis. 1996. Effects of Conservation Reserve Program field age on avian relative abundance, diversity, and productivity. Wilson Bulletin 108: 760-770.

Milchunas, D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. Journal of Vegetation Science 1: 375-384.

Milchunas, D.G. and W.K. Lauenroth. 2001. Belowground primary production by carbon isotope decay and long-term root biomass dynamics. Ecosystems 4: 139-150.

Oades, J.M. 1988. The retention of organic matter in soils. Biogeochemistry 5: 35-70.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Parton W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173–1179.

Paschke, M., T. McLendon, and E. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3: 144-158.

Post, W.M., W.R. Emanuel, P.J. Zinke, A.G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature 298: 156-159.

Post, W.M., and K.C. Kwon. 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6: 317-327.

Potter, K.N., H.A.Torbert, H.B. Johnson, and C.R.Tischler. 1999. Carbon storage after long-term grass establishment on degraded soils. Soil Science 164: 718-725.

Reeder, J.D., G.E. Schuman, and R.A. Bowman. 1998. Soil C and N changes on conservation reserve program lands in the Central Great Plains. Soil and Tillage Research 47: 339-349.

Robles, M.D., and I.C. Burke. 1997. Legume, grass, and Conservation Reserve Program effects on soil organic matter recovery. Ecological Applications 7: 345-357.

Robles, M.D., and I.C. Burke. 1998. Soil organic matter recovery on Conservation Reserve Program fields in Southeastern Wyoming. Soil Science Society of America Journal 62: 725-730.

Samuel, M.J. 1985. Growth parameter differences between populations of blue grama. Journal of Range Management 38: 339-342.

Savage, D.A., and H.E. Runyon. 1937. Natural revegetation of abandoned farmland in the central and southern Great Plains. Pages 178-182 *in* Grassland ecology. Section 1, Fourth international grassland congress. Aberystwyth, Great Britain.

Schimel, D. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1: 77-91.

Shantz, H.L. 1917. Plant succession on abandoned roads in eastern Colorado. Journal of Ecology 5: 19-42.

Skold, M.D. 1989. Cropland retirement policies and their effects on land use in the Great Plains. Journal of Production Agriculture 2: 197-201.

Stevens, P.R., and T.W. Walker. 1970. The chronosequence concept and soil formation. Quarterly Review of Biology 45: 333-350.

USDA Farm Service Agency. 2008. U.S. Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 26 October 2007). 4 November 2007 from: http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM

USDA National Agricultural Statistics Survey. 2008. Quick Stats: Agricultural Statistics Data Base. 4 November 2008 from: http://www.nass.usda.gov/QuickStats

Vinton, M.A., and I.C. Burke. 1995. Interactions between individual plant species and soil nutrient status in short grass steppe. Ecology 76: 1116-1133.

Vitousek, P.M., and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87-115.

Zeiter, M., A. Stampfli, and D.M. Newbery. 2006. Recruitment limitation constrains local species richness and productivity in dry grassland. Ecology 87: 942–951.

Chapter 2: Plant Community Dynamics on Conservation Reserve Program Lands in Northeastern Colorado

Introduction

Plant community composition is a key attribute of ecosystems that can provide insight into how species associate, function, and interact with each other and the abiotic environment. Changes in plant community composition occur in space due to environmental heterogeneity and in time with short-term fluctuations in plant populations and longer-term successional change (Delcourt et al. 1983, van der Maarel 1988). The spatial and temporal dynamics of plant community composition are influenced by disturbance, which disrupts community structure and increases the availability of resources (White and Pickett 1985). The subsequent processes of colonization and species replacement occur on a dynamic mosaic of patches in the landscape (Watt 1947) and are mediated by environmental conditions (Bazzaz 1979), availability of propagules (Egler 1954), and human activity (Westhoff 1971).

The impact disturbance has on plant community composition and trajectory of succession depends on characteristics of the disturbance (Sousa 1984, Coffin and Lauenroth 1988). Dryland (non-irrigated) wheat cropping is an extensive land use that utilized over one million hectares of former shortgrass steppe in Colorado during 2007 (USDA National Agricultural Statistics Service 2008). Tillage practices destroy above and belowground plant components at the field scale, unlike drought and grazing, to which shortgrass species have adapted (Milchunas et al. 1988). Seeding the field with an annually harvested crop replaces the diverse composition of perennial grasses, herbaceous dicots, subshrubs, and cacti. Cultivation also alters the physical and chemical characteristics of the soil (Burke et al. 1989), which can affect plant community dynamics.

Following the cessation of cropping, plant communities undergo succession. Without belowground perennial organs intact, plant establishment must occur from seeds that survived the disturbance or dispersed into the fields, or from vegetative spread from the edge of the field. Dispersal events are dependent on the location and reproductive traits of plants in the area surrounding the field, as well as site conditions for germination and establishment (Bazzaz 1979). Low precipitation and high potential evapotranspiration in the shortgrass steppe (Lauenroth and Bradford 2006) can limit plant establishment and growth, as well as the rate of succession through their influence on soil moisture. However, short-term wet-dry cycles drive fluctuations in species composition, especially in highly perturbed areas (Milchunas et al. 1990). Interactions among species and species modification of their environment can further contribute to changes in plant community composition during succession (Connell and Slatyer 1977).

Human activity can modify the trajectory of natural succession. The USDA Conservation Reserve Program (CRP) has converted cultivated land to perennial vegetation and currently includes nearly 1 million hectares in Colorado (USDA Farm Service Agency 2008). CRP land is seeded with perennial grasses and forbs, which can modify the rate of succession. Established perennial plant cover meets management objectives, including reduction in soil erosion and improvement of water quality (Skold 1989). Since allowable seed mixes may contain species and varieties that are not native to northeastern Colorado, CRP fields can have a plant community that is compositionally very different from undisturbed shortgrass steppe.

I constructed a general model of plant community dynamics on CRP fields to account for perennial grasses in the CRP seed mix (Burger et al. 1990, Millenbah et al. 1996) by modifying old-field succesional models developed in the shortgrass steppe (Judd and Jackson 1939, Costello 1944, Coffin et al. 1996). Like previous models, my modified model includes a forb and annual grass vegetation stage immediately following the cessation of cropping (Fig. 1). This stage is replaced by a seeded perennial grass stage and a subsequent colonizing perennial grass stage. Colonizing perennial grasses disperse from neighboring fields, with short-lived species establishing before long-lived shortgrasses (Savage and Runyon 1937, Judd 1974, Lauenroth and Milchunas 1992). I used the modified model to test the rate of development and the duration of persistence of each of these stages.

My objective was to determine plant community composition in CRP fields relative to undisturbed shortgrass steppe and to better understand the controls of plant community variability in these fields. Specifically, I addressed the following questions:

1) How does time since enrollment affect plant community composition in CRP fields?
2) How does seed mix affect plant community composition in CRP fields?
3) How does environmental variability affect interannual change in plant community composition in CRP fields and undisturbed shortgrass steppe?

Methods

Study sites

My study was conducted at undisturbed shortgrass steppe sites within the Central Plains Experimental Range (CPER, Shortgrass Steppe Long Term Ecological Research site) located 60 km northeast of Fort Collins, Colorado (40° 49' N, 107° 47' W), and CRP sites located within 13 km to the south and 3 km to the west of the CPER. The climate is semiarid with a long-term (1969-2007) mean annual precipitation of 332 mm ($\sigma = 99$ mm), 80% of which falls between April and September, and a mean annual temperature of 9.6°C ($\sigma = 1.1$ °C). Undisturbed shortgrass steppe has a long-term (1939-1990) mean annual aboveground net primary production of 97 g m^{-2} with a range of 62–143 g m^{-2} (Lauenroth and Sala 1992). These sites had been long-term moderately summer grazed, but I excluded them from grazing during the study.

I partitioned CRP sites into those seeded with perennial grasses native to northern Colorado and those planted with perennial grasses that are not native to northern Colorado (introduced). The native seed mix contained *Agropyron smithii*[*] (~ 30% weight of all seed), *Bouteloua gracilis* (~ 20%), *Bouteloua curtipendula* (~ 20%), other perennial grasses (~ 20%; *Nassella viridula*, *Schizachyrium scoparium*, *Panicum virgatum*, and *Sorghastrum nutans)* 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 time since CRP enrollment, I established a chronosequence (Stevens and Walker

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[*] plant nomenclature follows Great Plains Flora Association 1986

1970) that consisted of three field age classes: early, mid, and late. All fields in the chronosequence were seeded with a native seed mix to minimize differences in the potential vegetation. I sampled each field for 3 years to account for environmental variability. Early fields represented 2-4 years after CRP enrollment, mid fields represented 7-9 years after CRP enrollment, and late fields represented 18-20 years after CRP enrollment. To address the effect of using different seed mixes, I 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 three year study.

All fields were in a non-irrigated wheat-fallow rotation prior to CRP enrollment. The year of CRP enrollment, 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 (~ 0.5 g m^{-2} seed) 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 a similar topographic relief (< 3% slope). I replicated each of the six field types three times for a total of eighteen fields sampled (6 field types x 3 field replicates = 18 fields sampled).

Sampling Methods

I measured species composition in 40 ¼ m^2 circular quadrats in each field in late August/early September 2005, 2006, and 2007. Quadrats were spaced 20 m apart along 5 evenly-spaced transects and occurred a minimum of 100 m from the field edge to minimize edge effect. I estimated canopy cover class (0-1%, 1-5%, 5-15%, 15-25%, 25-40%, 40-60%, 60-100%) by species. Only plants that had grown during the sampling year were included. I took canopy cover estimates of *Bromus tectorum*, an introduced winter annual grass species, at the end of its growing season in early June. The canopy cover data for each species in each field type is included as Appendix A.

Statistical Analyses

I analyzed plant community composition by using the average canopy cover of each species in each field. I subsequently grouped species according to life form (grass, forb, cactus, and subshrub) in order to represent important reproductive and structural traits that can influence recovery and ecosystem function in the shortgrass steppe (Vinton and Burke 1995). I grouped grasses and forbs according to their lifespan (annual and perennial), and perennial grasses were further grouped according to whether or not they were seeded (seeded and colonizing). For separate analyses, I grouped species according to photosynthetic pathway (C3, C4, and CAM) and also according to whether or not they were native to northeastern Colorado (native and introduced). I calculated species density by taking the average number of species in a ¼ m^2 quadrat in each field. I performed repeated measures analysis of variance on the canopy cover of plant functional types and species density with field type as the main effect and year as the repeated measure modeled with autoregressive correlation structure (Proc Mixed, SAS 9.2, SAS Institute Inc. 2002-2008, Cary, NC, USA). Canopy cover data were arcsine square root transformed to meet assumptions of normality and homogeneity of variance. I used a Tukey multiple comparison adjustment when comparing field types separately for each year and years separately for each field type (Proc Glimmix, SAS, June 2006 release). I assumed a linear response of canopy cover of functional types across time since CRP enrollment and performed linear regression on all fields in the chronosequence (Proc Reg, SAS 9.2). A nonlinear model provided a better fit for annual grasses. Regressions were performed using canopy cover from individual years, not age classes, to collectively account for successional change and interannual variability in all CRP fields in the chronosequence. I report the coefficient of determination (r^2) to explain the amount of variability in canopy cover of functional types explained by time since CRP enrollment, but the p-value was not accurate because the regression was performed on untransformed data. I performed additional regressions between different functional types, as well as species density and annual precipitation in order to assess how the biotic and abiotic environments influenced recovery dynamics.

Results

Both inter- and intra-annual variability in precipitation was high during the study. Annual precipitation ranged from 301 mm in 2006 to 409 mm in 2007 (Table 1). Early growing season precipitation ranged from 54 mm in 2006 to 202 in 2005. Similarly, late growing season precipitation was 53 mm in 2005 and 224 in 2007. Early growing season precipitation in 2005 was 42% above the long-term mean and late growing season precipitation was 57% below the mean. 2006 and 2007 showed the opposite trends, with early growing season precipitation 62% and 42% below the mean and late growing season precipitation 16% and 81% above the mean, respectively.

Canopy cover of species and functional types were affected by time since CRP enrollment and seed mix. Annual and perennial forb canopy cover was high in the early CRP fields and decreased as time since CRP enrollment increased (collectively 0.86% per year, Fig. 2). Both these functional types had high interannual variability. Perennial forb canopy cover was on average six times lower than annual forb canopy cover in CRP fields during the study. Forb canopy cover in late CRP fields seeded with native perennial grasses was not significantly different from late CRP fields seeded with introduced perennial grasses or undisturbed shortgrass steppe for the first two years of the study, but was significantly higher in late fields seeded with *Agropyron intermedium* in 2007.

Annual grass canopy cover increased and reached a peak of 39% 7 years after CRP enrollment before declining to almost no canopy cover within 18 years after CRP enrollment (Fig. 3). This increase was almost entirely due to the introduced winter annual, *Bromus tectorum*, which had high spatial and temporal variability in canopy cover. Other annual grasses had high canopy cover in early CRP fields and were nearly absent in mid CRP fields. All annual grass canopy cover in late CRP fields seeded with native perennial grasses was < 1% in all sampling years and was not significantly different from either of the late CRP fields seeded with introduced perennial grasses or undisturbed shortgrass steppe.

Seeded perennial grass canopy cover increased 1.3% per year along the chronosequence (Fig. 4). Seeded perennial grass canopy cover approached 30% in late CRP fields seeded with native perennial grasses, which was not significantly different from either of the late CRP fields seeded with introduced perennial grasses for all sampling years. However, seeded perennial grass canopy cover in CRP fields was significantly lower than perennial grass canopy cover in undisturbed shortgrass steppe for all sampling years. Colonizing perennial grass canopy cover increased 0.50% per year along the chronosequence, but was near zero for the first 4 years of CRP enrollment (Fig. 5). Late CRP fields seeded with introduced perennial grasses were not significantly different from late CRP fields seeded with native perennial grasses in colonizing perennial grass canopy cover for all sampling years, but increased in canopy cover during the study. Interannual variability was low for seeded and colonizing perennial grasses relative to forbs and annual grasses. Dwarf shrubs and cacti were absent in CRP fields, except in late fields seeded with native perennial grasses, where they occurred with < 1% canopy cover (not shown).

In 2005, there was significantly higher relative canopy cover of C3 species and lower relative canopy cover of C4 species in all CRP fields, except late CRP fields seeded with native perennial grasses, compared to undisturbed shortgrass steppe (Fig. 6). Along the chronosequence, C3 canopy cover was significantly higher in mid CRP fields than late CRP fields. All CRP fields showed a trend of decreasing C3 and increasing C4 relative canopy cover in the three years of the study (only mid CRP fields seeded with native perennial grasses and late CRP fields seeded with *Agropyron intermedium* were significant), while undisturbed shortgrass steppe remained a C4 dominated plant community. C3 dominance diminished even in CRP fields seeded with introduced C3 species over the three-year study period. By 2007, the relative canopy cover of C3 species was only higher in mid CRP fields and late CRP fields seeded with *Bromus inermis* relative to undisturbed shortgrass steppe.

Plants with a CAM photosynthetic pathway were only present in undisturbed shortgrass steppe and late CRP fields seeded with native perennial grasses.

Many CRP fields were composed of significantly more introduced species than undisturbed shortgrass steppe (Fig. 7). Mid CRP fields had the highest canopy cover of introduced species along the chronosequence, which were not significantly different from late CRP fields seeded with introduced perennial grasses in all years of the study. However, there was an increase of native species canopy cover in late CRP fields seeded with introduced perennial grasses. Late CRP fields seeded with native perennial grasses had > 90% relative canopy cover of native species, and were not significantly different than undisturbed shortgrass steppe.

Species density (number of species / $0.25m^2$) decreased along the chronosequence in all years of the study. Late CRP fields seeded with introduced perennial grasses had significantly lower species density than late CRP fields seeded with native perennial grasses in 2005, but were not lower in 2006 and only late fields seeded with *Bromus inermis* were lower in 2007. Species density in undisturbed shortgrass steppe was not significantly different from CRP fields seeded with native perennial grasses, except in 2005 when it was significantly higher. There was interannual variability in species density within field types. Undisturbed shortgrass steppe and CRP fields seeded with native perennial grasses had low species in 2006 relative to the other two sampling years (statistically significant in undisturbed shortgrass steppe and mid CRP fields). There was significantly higher species density in late CRP fields seeded with *Agropyron intermedium* in 2007 compared to the other two sampling years.

Discussion

Time since CRP enrollment affected plant community composition. Early CRP fields underwent succession and the plant community was likely influenced by the seed bank and seed dispersal. Seed mix determined which perennial grasses dominated the plant community within 18 years, but variable establishment allowed for dominance by plants with different life forms, photosynthetic pathways, and origins. Species density declined in CRP fields as seeded perennial grass cover increased and was lowest in late CRP fields seeded with introduced perennial grasses. Relative differences in canopy cover between species and functional types in these fields were modified by shifts in the amount and seasonality of precipitation. Low mean annual precipitation and the spread of colonizing perennial grasses are likely to affect plant community composition beyond 20 years in CRP fields.

The dominance by forbs and annual grasses in early and mid CRP fields followed my model of plant community dynamics. The success of these functional types may be attributed to their prolific seed production, rapid dispersal mechanisms, and high abundance in shortgrass steppe seedbanks (Coffin and Lauenroth 1989). Forbs generally declined as time since CRP enrollment increased and were inversely correlated to perennial grass canopy cover across all CRP fields in the first two years of the study ($r = 0.77$, $P = 0.0002$). This suggests that the increased dominance of perennial grasses inhibited forb canopy cover, which has been indirectly shown through perennial grass removal and disturbance studies in the shortgrass steppe (Coffin 1988, Hardwicke 2006, Munson and Lauenroth, in press). However, forb canopy cover had high interannual variability, even in late CRP fields that had relatively high perennial grass cover. Precipitation can be a strong driver of forb canopy cover and abundance in semiarid grasslands. In CRP fields, above average late growing season (July-September) precipitation in 2007 likely caused the increase in canopy cover of primarily late-growing annual forbs through an increase in soil moisture. Native and introduced members of Chenopodiaceae (*Salsola iberica*, *Kochia scoparia*, and *Chenopodium* spp.) were largely responsible for this increase. These species have been shown to increase in disturbed shortgrass steppe (Milchunas and Lauenroth 1995), including abandoned cropland (Costello 1944). High annual precipitation may allow forb species to overcome the competitive suppression of grasses, since there was no longer a significant inverse relationship between the two functional types in 2007.

Annual grasses were present within 2 years after CRP enrollment, but there was low canopy cover (< 0.4%) of *Bromus tectorum*. Annual grass species continued to colonize early CRP fields and most species reached a peak within 4 years. However, *B. tectorum* continued to increase with 11% canopy cover after 4 years and 39% in 7 year CRP fields. This suggests that the presence of *B. tectorum* causes higher annual grass canopy cover and a prolonged annual grass dominance in CRP fields compared to what was predicted in the model. Although undisturbed shortgrass steppe has a low invasion of *B. tectorum* (Bradford and Lauenroth 2006), CRP fields are susceptible until perennial grasses dominate the plant community. Invasion of this introduced annual grass showed high spatial variability, as indicated by a range of < 1% to 30% canopy cover in CRP fields 4 years after enrollment. This variability was unlikely due to management practices since early CRP fields were operated and seeded by the same landowner and there was no weed control in any of the CRP fields. Fields may have differed in the nearest propagule source or propagule pressure from neighboring fields. Spatial variability among fields was still high 7 years after CRP enrollment, but all of these fields had > 25% *B. tectorum* canopy cover. Above average early growing season precipitation in March and April may have contributed to a significantly higher *B. tectorum* canopy cover in mid CRP fields in 2005, relative to the subsequent 2 years. The low canopy cover of annual grasses (< 1%) in all late CRP fields suggests that perennial grasses may have competitively excluded them. Low *B. tectorum* canopy cover even occurred in late CRP fields seeded with introduced grasses, which potentially had more open niche space for invasion (Crawley 1987) with half as much total vegetation canopy cover and lower species richness.

Consistent with the model, seeded perennial grasses successfully germinated and reached a canopy cover of 10% within four years of CRP enrollment (three years after seeding). Although there was low variability among early CRP fields in seeded perennial grass canopy cover, this may be attributed to similar seeding conditions by the same operator and is not necessarily reflective of similar perennial grass establishment on all early CRP fields, which can have high spatial and temporal variability (McCoy et al. 2001, Bakker et al. 2003). An increase in seeded perennial grass canopy cover of approximately 1% per year is slow relative to a 10-15% per year increase reported for cultivated land converted to grasslands in more mesic regions (Baer et al. 2002, Camill et al. 2004). Although seeded perennial grasses composed a majority of the canopy cover after 18 years, it was under half the perennial grass cover found in undisturbed shortgrass steppe and was variable among fields. This indicates a lack of full perennial grass recovery from CRP seeding practices. Canopy cover of seeded introduced perennial grasses was similar to native perennial grasses after 18 years, suggesting that introduced grasses can endure some drought conditions (Sheaffer et al. 1992). However, there is evidence that these grasses may not always persist over the long-term.

Recovery of the dominant perennial shortgrass, *B. gracilis*, is of particular importance because it composes 75-90% of production at most undisturbed sites (Coffin and Lauenroth 1988), and is therefore a major control on structure and function in the shortgrass steppe (Hyder et al. 1975, Burke et al. 1995). There is typically slow recovery of *B. gracilis* on abandoned cropland (Klipple and Costello 1960), but seed availability (Coffin and Lauenroth 1989) and competition from perennial plants (Aguilera and Lauenroth 1993) are not limitations in CRP fields. Furthermore, soil moisture and temperature requirements for *B. gracilis* germination (Lauenroth et al. 1994) may be more common in CRP fields, which have less plant cover, than in undisturbed shortgrass steppe. These factors likely contributed to the establishment and growth of 2% *B. gracilis* canopy cover in early CRP fields and 8% canopy cover in late CRP fields over the course of the study. Despite an increase, late CRP fields had only a quarter of the *B. gracilis* canopy cover compared to undisturbed shortgrass steppe and there was high variability in canopy cover among fields. Canopy cover of *B. gracilis* can still be lower in fields 50 years after the cessation of cropping relative to undisturbed shortgrass steppe (Coffin et al. 1996). Furthermore, *B. gracilis* canopy cover was < 1% on 7, 8, and 9 year old CRP fields.

This reinforces the idea that shortgrass recovery can be extremely slow and variable (Hyder et al. 1971, Coffin et al. 1996), even when they are seeded. Low canopy cover on mid CRP fields may have been due to field preparation and seeding methods (personal communication with landowner). Low water availability is a less likely explanation, since there was above average precipitation the year these fields were seeded.

My model of plant community dynamics predicted that colonizing perennial grasses would establish after seeded perennial grasses because they were not in the soil seed bank and have high interannual variability in establishment (Costello 1944). The rate of increase of colonizing perennial grass cover is important because it indicates the recovery potential of abandoned fields in the absence of CRP management practices. Colonizing perennial grasses were not present in the first 4 years after CRP enrollment and increased at a slower rate than seeded perennial grasses. *Sporobolus cryptandrus* and *Aristida purpurea*, both prolific seed producers, accounted for nearly all the colonizing perennial grass in CRP fields. These short-lived grasses are subdominants in the shortgrass steppe and typically become more common following disturbance (Costello 1944, Milchunas et al. 1990, Munson and Lauenroth, in press). Colonizing perennial grasses increased by over 300% in late CRP fields during the course of the study and are likely to continue to propagate in fields in which adult plants have become established. They equally colonized fields seeded with introduced and native perennial grasses, indicating that introduced perennial grasses did not exclude the colonization and spread of native perennial grasses. There is evidence that colonizing perennial grasses replace seeded perennial grasses, which fits model predictions. A late CRP field seeded with *Bromus inermis* and a late CRP field seeded with *Agropyron intermedium* completely turned over from dominance by the respective introduced grass to dominance by colonizing perennial grasses over the study period. However, no shortgrasses colonized these fields, and shrubs and cacti were only present in CRP fields after 18 years of CRP enrollment, which supports model predictions that these functional types are slow to recover (Coffin et al. 1996).

Plant community composition in CRP fields included a high proportion of C3 species, which represented an important physiological and phenological difference from the undisturbed shortgrass steppe. This difference in composition is important because it has the potential to influence ecosystem processes (Tilman et al. 1997, Epstein et al. 1999). Along the chronosequence, early CRP fields were composed of many C3 forbs and the annual C3 grass, *Bromus tectorum*, which transitioned to seeded C4 perennial grasses if a native seed mix was used. After 18 years, CRP fields seeded with native perennial grasses were not significantly different from undisturbed shortgrass steppe in the proportion of C4 species. However, CRP fields were dominated by C3 species after 18 years if they were seeded with *Bromus inermis* and *Agropyron intermedium*, which are both C3 perennial grasses.

Plant community dynamics may also be sensitive to changes in environmental conditions, which can cause a shift in the proportion of C3 and C4 species (MacGillvary et al. 1995, White et al. 2000, Morgan et al. 2004). Model simulations indicate that a change in the seasonal pattern of precipitation can alter the composition of C3 and C4 plants at a decadal time scale in the northernmost region of the shortgrass steppe (Epstein et al. 1999). My study reveals that there can be fluctuations in composition in CRP fields at a much shorter time scale. Within 3 years, all CRP fields shifted towards a higher proportion of C4 species despite little interannual variability in the dominance of C4 species in undisturbed shortgrass steppe. While the establishment of seeded C4 perennial grasses contributed to this response in the chronosequence, colonizing C4 perennial grasses and late-growing C4 forbs increased in all CRP fields. Growth of these functional types was facilitated by a shift to high late growing season precipitation in 2006 and 2007. Low early growing season precipitation, in the same years, may have reduced growth and competition from early-growing C3 species. Some fields seeded with introduced C3 perennial grasses had a doubling of C4 species canopy cover, which indicates that C3 dominated plant communities may not be able to persist for the long-term in this region.

The near absence of introduced species on undisturbed shortgrass steppe suggests that they require disturbance to establish (Milchunas and Lauenroth 1995). Introduced species were present on all early CRP fields, but the rate at which they spread in the first four years after CRP enrollment was highly variable (from a 1% decrease to 17% increase). This was more likely dependent on propagule pressure rather than on site conditions, which were the same in early CRP fields. Seven years after CRP enrollment, introduced species were high (> 35% canopy cover) in all fields, largely due to the presence of *Bromus tectorum*. High *B. tectorum* canopy cover in mid CRP fields may have contributed to low relative canopy cover of native species due to depletion of resources (Melgoza et al. 1990, Lowe et al. 2003, Booth

2003). This is supported by a significant negative correlation between native seeded perennial grass canopy cover and *B. tectorum* canopy cover ($r = 0.76$, $P = 0.02$) in all mid CRP fields across all years of the study. Despite the potential for competition with *B. tectorum*, native perennial grasses successfully germinated with low canopy cover of *B. tectorum* in early CRP fields. There was high canopy cover of native species (> 90%) in late CRP fields seeded with native perennial grasses, which indicates that introduced species were competitively suppressed in the long-term. Even fields dominated by the seeded introduced perennial grasses were composed of half native species by the end of the study. This was because adjacent undisturbed shortgrass steppe provided a native seed source for CRP fields (Coffin et al. 1996).

Natural succession on abandoned cropland can result in a gradual accretion of species (Tilman 1990), but seeding perennial grasses following abandonment in the Great Plains has resulted in no change (Camill et al. 2004) or a decrease (Burger et al. 1990, Millenbah et al. 1996, McCoy et al. 2001) in species richness through time, presumably due to the increased dominance of seeded perennial grasses. Early stages of plant community development in CRP fields included a high coexistence of different plant functional types, which resulted in high species density. Plant community composition at this stage was determined by the seedbank and stochastic dispersal events of native and introduced species from nearby fields. Composition became more deterministic, as seeded perennial grasses established and dominated CRP fields within 18 years. Perennial grasses may have competitively suppressed other functional types, which resulted in low species density in late CRP fields. A lack of recruitment can be common once grasses establish in restorations (Brown and

Bugg 2001, Zeiter et al. 2006, Foster et al. 2007), especially forb species that compose most of the species richness. Low propagule availability of certain species of native forbs in CRP fields seems likely given that 63% of the native annual and perennial forbs that occurred in undisturbed shortgrass steppe were not present in the oldest CRP fields seeded with native perennial grasses. Many of these forbs were extremely rare or had slow dispersal mechanisms. Furthermore, germination and establishment of species from seed may be less likely in fields that had high canopy cover of existing vegetation due to competition and limiting environmental conditions (Aguilera and Lauenroth 1993, Lauenroth et al. 1994, Singh et al. 1996).

Species density was lower in fields seeded with introduced perennial grasses than fields seeded with native perennial grasses in 2005. Introduced species can displace native species and reduce species richness (Wilson 1988, D'Antonio and Vitousek 1992). Christian and Wilson (1999) found that fields in the northern mixed prairie seeded seeded with *Agropyron cristatum*, an introduced perennial grass contained fewer native species, resulting in lower species richness and diversity than fields that had undergone succession to native perennial grasses. Reduction of *A. cristatum* increased native grass establishment and the richness and canopy cover of other native species, in part due to increased moisture and nitrogen availability (Bakker et al. 2003). Similar mechanisms may limit native species canopy cover in the shortgrass steppe. The rhizomatous growth of introduced perennial grasses in this study may exploit horizontal soil resource space more uniformly than caespitose grasses (Derner and Briske 2001), thereby reducing the belowground resource space for other functional types.

Interannual changes in species density in CRP fields seeded with native perennial grasses and undisturbed shortgrass steppe were correlated to annual precipitation ($r = 0.43$, $P = 0.009$). This is expected in a region where plant growth is constrained by water availability (Noy-Meir 1973). Annual forb species, which can respond rapidly to changes in water availability (Milchunas et al. 1990), were largely responsible for interannual variability in species density. Late CRP fields seeded with introduced perennial grasses had low species density, except in 2007, when species density increased in fields seeded with *Agropyron intermedium*. Most of the species responsible for high species density in these fields were native. Therefore, it is possible for native species to recolonize fields where introduced species dominated (Seabloom et al. 2003), especially in years when annual precipitation is above the mean.

Within a regional patchwork of land uses, CRP fields are an important transition between annual cropping systems and native shortgrass steppe. They are connected to each other and other land uses by dispersal vectors (Watt 1947) and bring new species and provide habitat for rare species across the landscape. Variation in these plant communities is driven by time since CRP enrollment, seed mix, and environmental variability. Understanding the patterns and drivers of plant community composition at a regional scale contributes to the knowledge of the effects of land use change in the shortgrass steppe.

Literature Cited

Aguilera, M.O., and W.K. Lauenroth. 1993. Neighborhood interactions in a natural population of perennial bunchgrass *Bouteloua gracilis*. Oecologia 94: 595-602.

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12: 1688-1701.

Bakker, J.D., S.D. Wilson, J.M. Christian, X.D. Li, L.G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13: 137-153.

Bazzaz, F.A. 1979. Physiological ecology of plant succession. Annual Review of Ecology and Systematics 10: 351–371.

Booth M.S. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. Journal of Ecology 91: 36–48.

Bradford, J.B., and W.K. Lauenroth. 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance, and seed availability. Journal of Vegetation Science 17: 693-704.

Brown, C.S., and R.L. Bugg. 2001. Effects of established perennial grasses on introduction of native forbs in California. Restoration Ecology 9: 38-48.

Burger, L.W., Jr. E.W. Kurzejeski, T.V. Dailey, and M.R. Ryan. 1990. Structural characteristics of vegetation in CRP fields in northern Missouri and their suitability as bobwhite habitat. Transactions of the North American Wildlife and Natural Resources Conference 55: 74-83.

Burke, I.C., C.M. Yonker, V.V. J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989. Texture, climate and cultivation effects on soil organic matter content in US grassland soils. Soil Science Society of America Journal 53: 800–805.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program. Ecological Applications 5: 793–801.

Camill, P., M.J. McKone, S.T. Sturges, W.J. Severud, E. Ellis, J. Limmer, C.B. Martin, R.T. Navartil, A.J. Purdie, B.S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14: 1680-1694.

Christian, J.M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. Ecology 80: 2397-2407.

Coffin, D.P. 1988. Gap-phase dynamics and succession in the shortgrass steppe. Dissertation, Colorado State University, Fort Collins, Colorado.

Coffin D. P., and W.K. Lauenroth. 1988. The effects of disturbance size and frequency on a shortgrass community. Ecology. 69: 1609–1617.

Coffin, D.P., and W.K. Lauenroth. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. American Journal of Botany 76: 53-58.

Coffin, D.P., W.K. Lauenroth, and I.C. Burke. 1996. Recovery of Vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications 6: 538-555.

Connell, J.H., and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Costello, D.F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. Ecology 25: 312-326.

Crawley, M.J. 1987. What makes a community invasible? Pages 429-454 in M.J. Crawley, P.J. Edwards, and A.J. Gray, eds. Colonization, sucession and stability. Blackwell, Oxford.

D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63-87.

Delcourt, H.R., P.A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. Quarterly Science Review 1: 153-175.

Derner, J.D., and D.D. Briske. 2001. Below-ground carbon and nitrogen accumulation in perennial grasses: A comparison of caespitose and rhizomatous growth forms. Plant and Soil 237: 117-127.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio. 4: 412-417.

Epstein, H.E., I.C. Burke, and W.K. Lauenroth. 1999. Response of the shortgrass steppe to changes in rainfall seasonality. Ecosystems 2: 139-150.

Foster, B.L., C.A. Murphy, K. Keller, T. Aschenbach, E.J. Questad, and K. Kindscher. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. Restoration Ecology 15: 652-661.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS.

Hardwicke, K. 2006. Prairie dogs, plants, and pollinators: tri-trophic interactions affect plant-insect floral visitor webs in shortgrass steppe. Dissertation, Colorado State University, Fort Collins, Colorado.

Hyder, D.N., Everson, A.C. and Bement, R.E. 1971. Seedling morphology and seeding failures with blue grama. Journal of Range Management 24: 287-292.

Hyder, D.N., R.E. Bement, E.E. Remmenga, and D.F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. USDA Technical Bulletin 1503.

Judd, I.B. 1974. Plant succession of old fields in the Dust Bowl. Southwestern Naturalist 19: 227-239.

Judd, I.B., and M.L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. American Society of Agronomy Journal 39: 541-547.

Klipple, G.E., and D.F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on shortgrass ranges of the Central Great Plains. U.S. Department of Agriculture Research Services Technical Bulletin 1216.

Lauenroth, W. K., and Milchunas, D. G. 1992. Short-grass steppe. Pages 183-226 *in* Coupland, R. T., ed. Ecosystems of the World 8A, Natural Grasslands, Introduction and Western Hemisphere. Elsevier, New York.

Lauenroth, W.K., and O.E. Sala. 1992. Long term forage production of North American shortgrass steppe. Ecological Applications 2: 397-403.

Lauenroth W.K., Sala O.E., Coffin D.P. & Kirchner T.B. 1994. The importance of soil water in the recruitment of Bouteloua gracilis in the shortgrass steppe. Ecological Applications 4: 741-749.

Lauenroth, W. K., and J. B. Bradford. 2006. Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. Ecosystems 9: 1-15.

Lowe, P. N., W.K. Lauenroth, and I.C. Burke. 2003. Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. Plant Ecology 167: 247-254.

MacGillivray, C.W., J.P. Grime, and I.S.P. Team. 1995. Testing predictions of the resistance and resilience of vegetation subjected to extreme events. Functional Ecology 9: 640-649.

McCoy, T.D., E.W. Kurzejeski, L.W. Burger Jr., and M.R. Ryan. 2001. Effects of Conservation practice, mowing, and temporal changes on vegetation on CRP fields in northern Missouri. Wildlife Society Bulletin 29: 979-987.

Melgoza, G., R.S. Nowak, and R.J. Tausch. 1990. Soil water exploration after fire: competition between Bromus tectorum and two native species. Oceologia 83: 7-13.

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., W.K. Laurenroth, P.L. Chapman and M.K. Kazempour. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. Journal of Vegetation Science 1: 375–384.

Milchunas, D.G., and W.K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient enrichment stress. Ecological Applications 5: 452-458.

Millenbah, K.F., S.R. Winterstein, H. Campa III, L.T. Furrow, and R.B. Minnis. 1996. Effects of Conservation Reserve Program field age on avian relative abundance, diversity, and productivity. Wilson Bulletin 108: 760-770.

Munson, S. M., and W. K. Lauenroth. In Press. Plant population and community responses to removal of the dominant species. Journal of Vegetation Science.

Morgan, J.A., A.R. Mosier, D.G. Milchunas, D.R. LeCain, J.A. Nelson, and W.J. Parton. 2004. CO_2 enhances productivity, alters species composition, and reduces forage digestibility of shortgrass steppe vegetation. Ecological Applications 14: 208-219.

Natural Resources Conservation Service. 1991. Technical Guide, Section IV, Standards and Specifications, Range Seeding, Colorado. USDA, Colorado.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics. 4:25-51.

Savage, D.A. and H.E. Runyon. 1937. Natural revegetation of abandoned farmland in the central and southern Great Plains. Pages 178-182 *in* Grassland ecology. Section 1, Fourth international grassland congress. Aberystwyth, Great Britain.

Seabloom, E.W., W.S. Harpole, O.J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences 100: 13384–13389.

Sheaffer, C.C., P.R. Peterson, M.H. Hall, and J.B. Stordahl. 1992. Drought effects on yield and quality of perennial grasses in the North Central United States. Journal of Production Agriculture 5: 556-561.

Singh, J.S., P. Bourgeron, P., and W.K. Lauenroth. 1996. Plant species richness and species-area relations in a shortgrass steppe in Colorado. Journal of Vegetation Science 7: 645-650.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.

Stevens, P.R., and T.W. Walker. 1970. The chronosequence concept and soil formation. Quarterly Review of Biology 45: 333-350.

Skold, M.D. 1989. Cropland retirement policies and their effects on land use in the Great Plains. Journal of Production Agriculture 2: 197-201.

Tilman, D. 1990. Constraints and tradeoffs: towards a predictive theory of competition and succession. Oikos 58: 3-15.

Tilman, D., J. Knops, D. Wedin, R. Peter, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302.

USDA Farm Service Agency. 2008. U.S. Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 27 June 2008). 4 November 2008 from: http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM

USDA National Agricultural Statistics Survey. 2008. Quick Stats: Agricultural Statistics Data Base. 4 November 2008 from: http://www.nass.usda.gov/QuickStats

Van der Maarel, E. 1988. Vegetation dynamics: patterns in time and space. Vegetatio 47: 259-265.

Vinton, M.A., and I.C. Burke. 1995. Interactions between individual plant species and soil nutrient status in short grass steppe. Ecology 76: 1116-1133.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1-22.

Westhoff, V. 1971. Choice and management of nature reserves in the Netherlands. Bulletin du Jardin Botanique National de Belgique 41: 231-245.

White, P.S., and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an Introduction. Pages 3-13 *in* S.T.A. Pickett and P.S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

White, T.A., B.D. Campbell, P.D. Kemp, and C.L. Hunt. 2000. Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. Global Change Biology 6: 671-684.

Wilson, S.D. 1988. The suppression of native prairie by alien species introduced for revegetation. Landscape and Urban Planning 17: 113-119.

Zeiter, M., A. Stampfli, and D.M. Newbery. 2006. Recruitment limitation constrains local species richness and productivity in dry grassland. Ecology 87: 942–951.

Year	2005	2006	2007	38-year Average
Annual Precipitation (Jan-Dec)	370	301	409	332
Early Growing Season Precipitation (Apr-Jun)	202	54	82	143
Late Growing Season Precipitation (Jul-Sep)	53	144	224	124

Table 1. Annual and seasonal precipitation (mm) from 2005-2007.

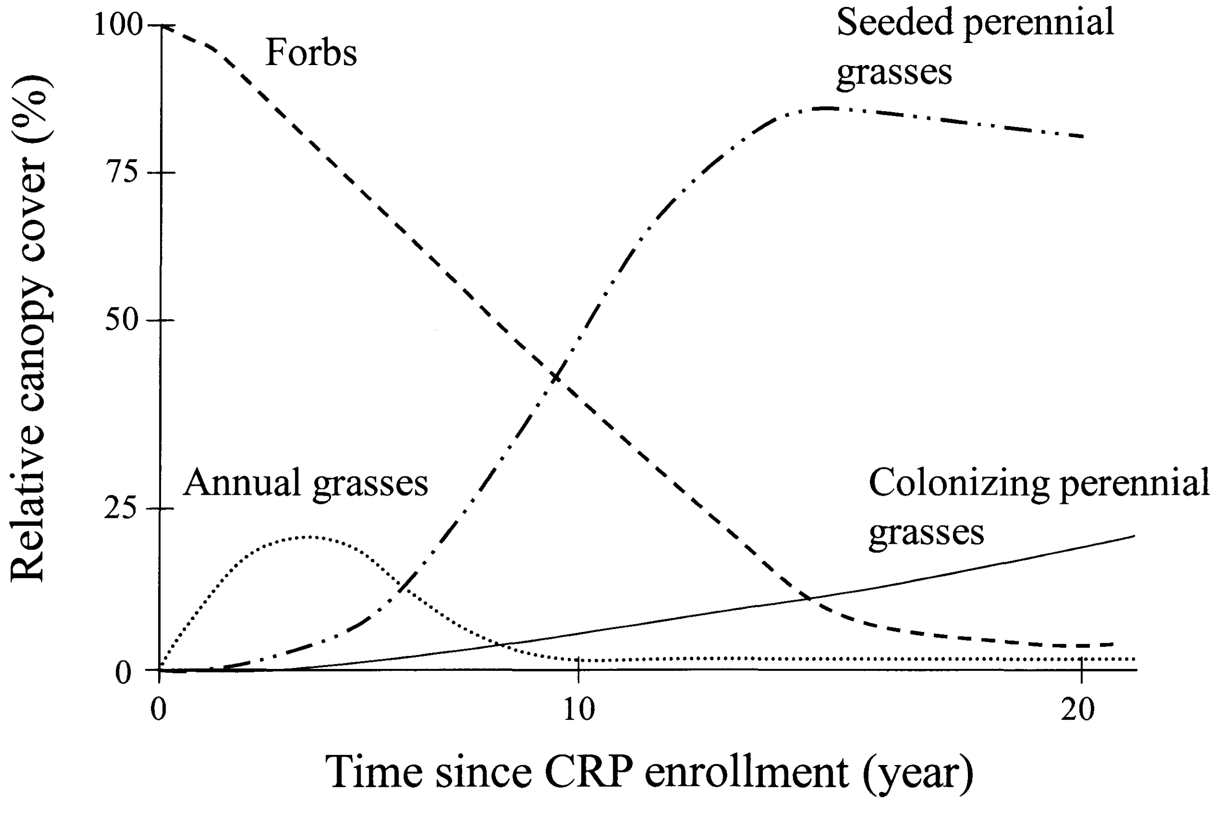

Figure 1. Model of plant community dynamics on CRP fields (modified from Coffin et al. 1996), which shows the trajectory of plant functional types (forbs, annual grasses, seeded perennial grasses, and colonizing perennial grasses) through time since CRP enrollment.

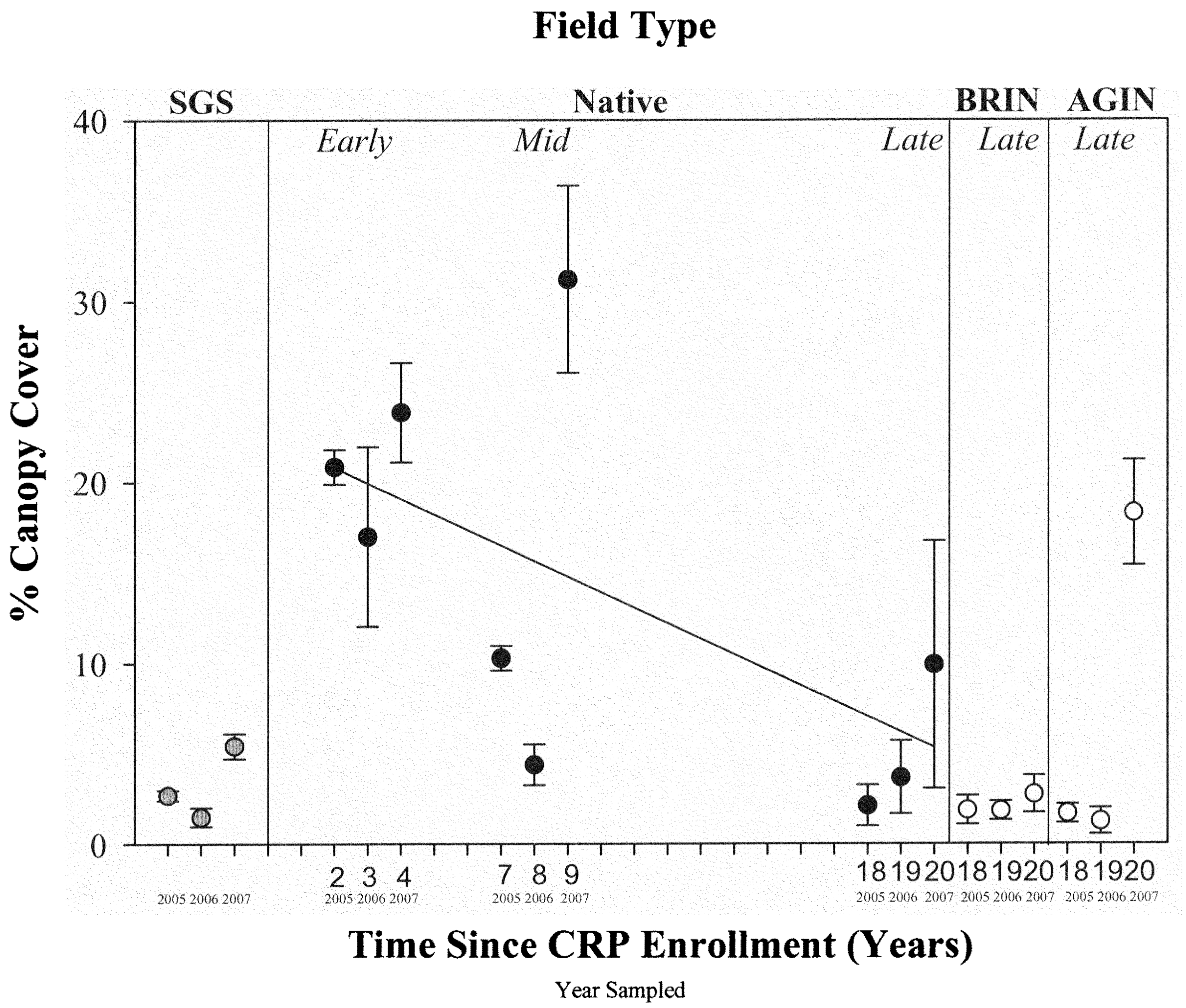

Figure 2. Mean percent canopy cover (± SE) of forbs in shortgrass steppe (SGS), and in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Chronosequence linear regression: y = -0.86x + 22, r^2 = 0.29.

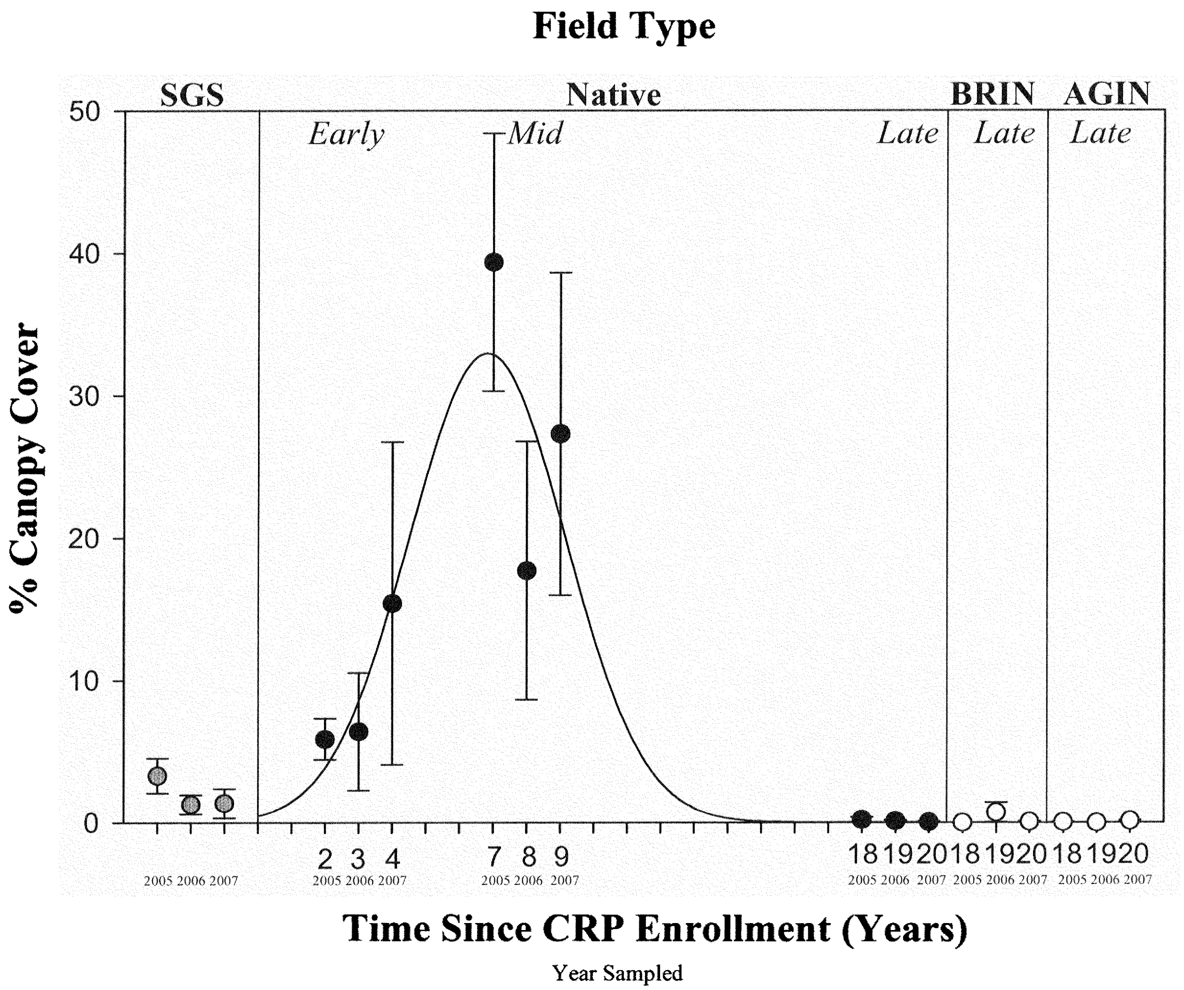

Figure 3. Mean percent canopy cover (± SE) of annual grasses in shortgrass steppe (SGS), and in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Chronosequence nonlinear regression: $y = 33e^{-0.5(\frac{x-6.8}{2.3})^2}$, $r^2 = 0.54$.

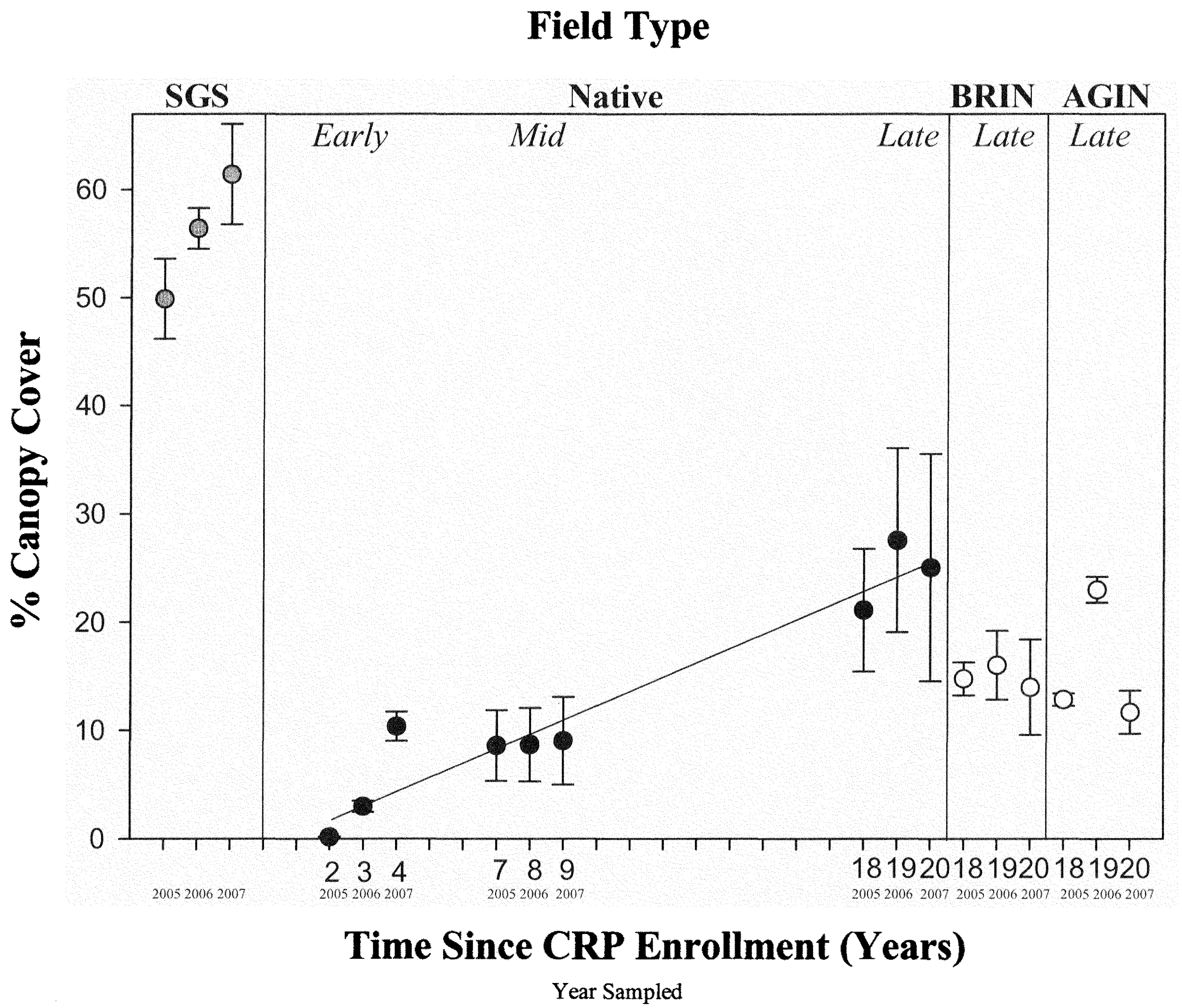

Figure 4. Mean percent canopy cover (± SE) of perennial grasses in shortgrass steppe (SGS), and seeded perennial grasses in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Chronosequence linear regression: $y = 1.3x - 0.39$, $r^2 = 0.55$.

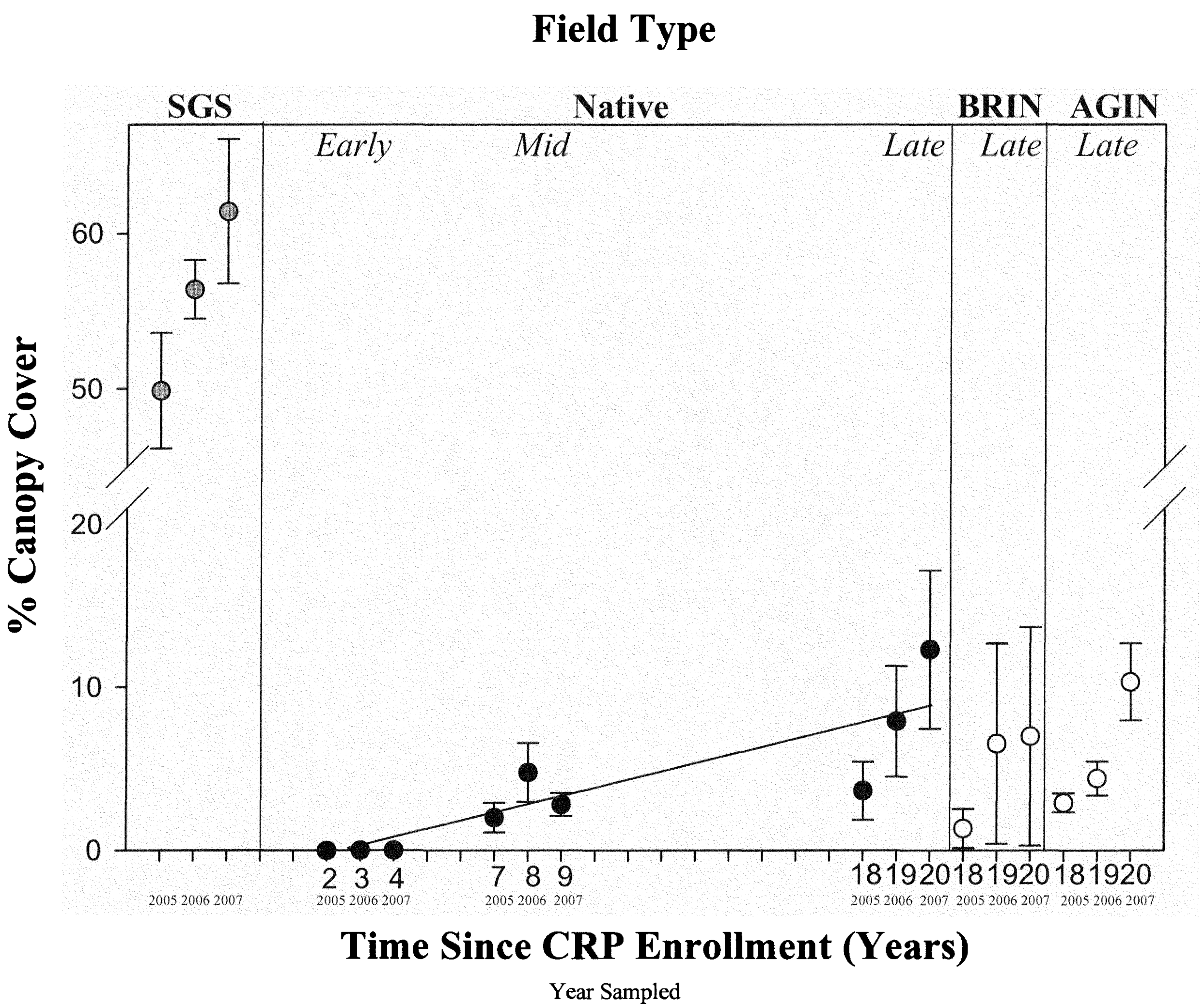

Figure 5. Mean percent canopy cover (± SE) of perennial grasses in shortgrass steppe (SGS), colonizing perennial grasses in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Chronosequence linear regression: $y = 0.50x - 1.3$, $r^2 = 0.46$.

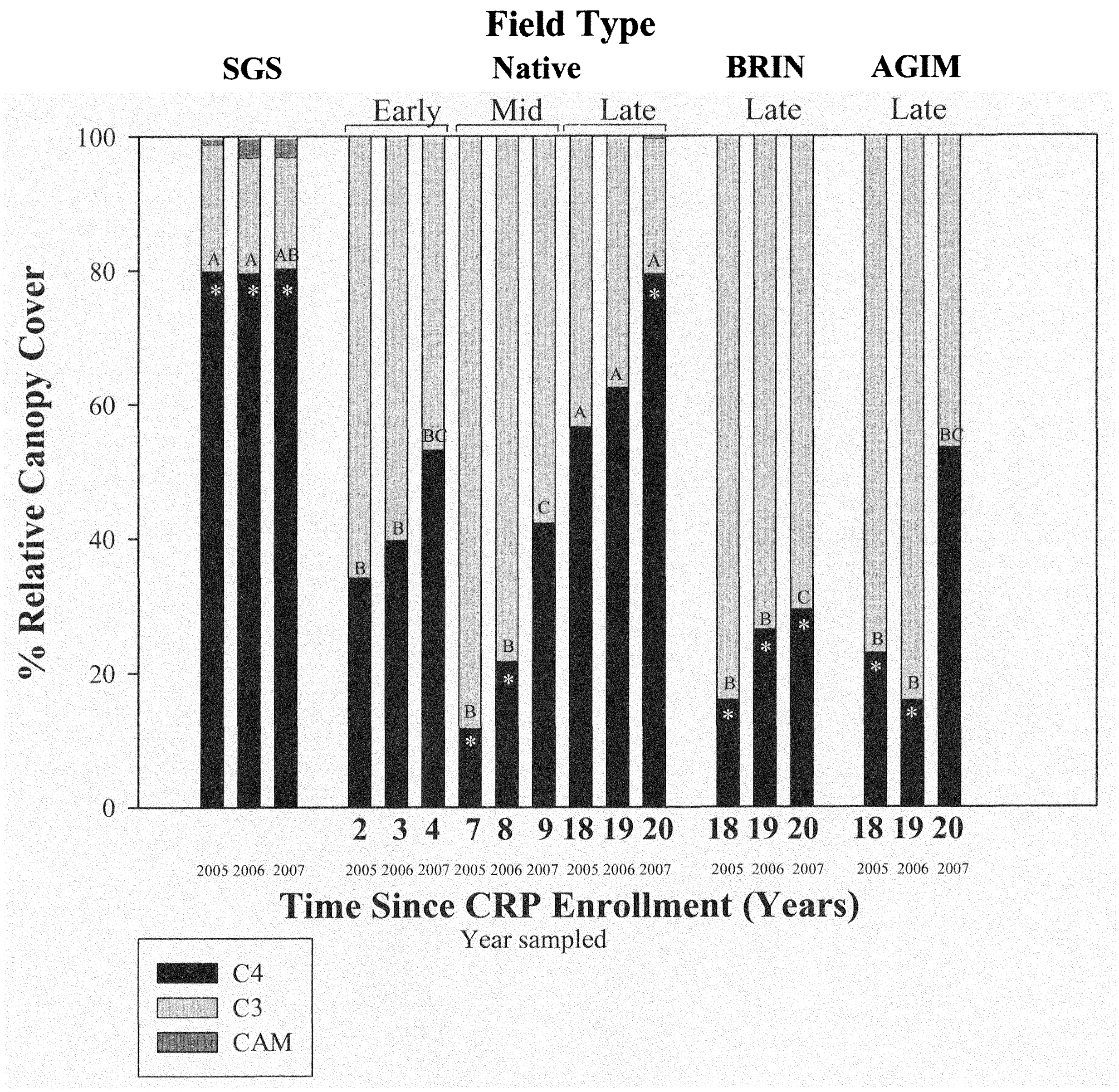

Figure 6. Percent relative canopy cover of plants with C3, C4, and CAM photosynthetic pathways in the shortgrass steppe (SGS) and in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Different capital letters designate significant differences (Tukey adjusted $P < 0.05$) in C3 and C4 composition among field types within the same sampling year and an asterix (*) designates significant differences ($P < 0.05$) between plants with C3 and C4 composition within the same field type in a sampling year.

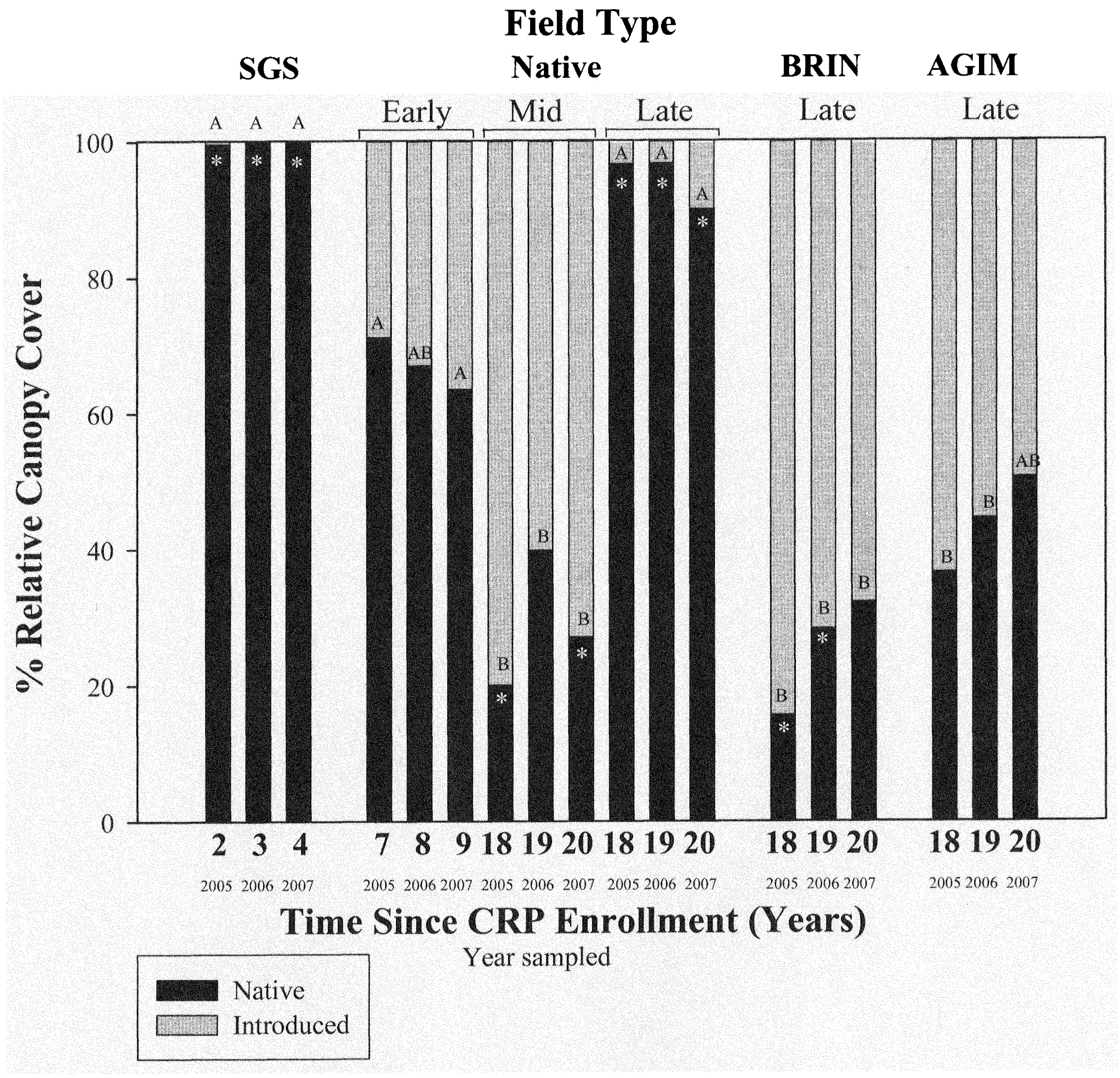

Figure 7. Percent relative canopy cover of native and introduced plants in the shortgrass steppe (SGS) and in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Different capital letters designate significant differences (Tukey adjusted $P < 0.05$) in native and introduced composition among field types within the same sampling year and an asterix (*) designates significant differences ($P < 0.05$) between plants with native and introduced composition within the same field type in a sampling year.

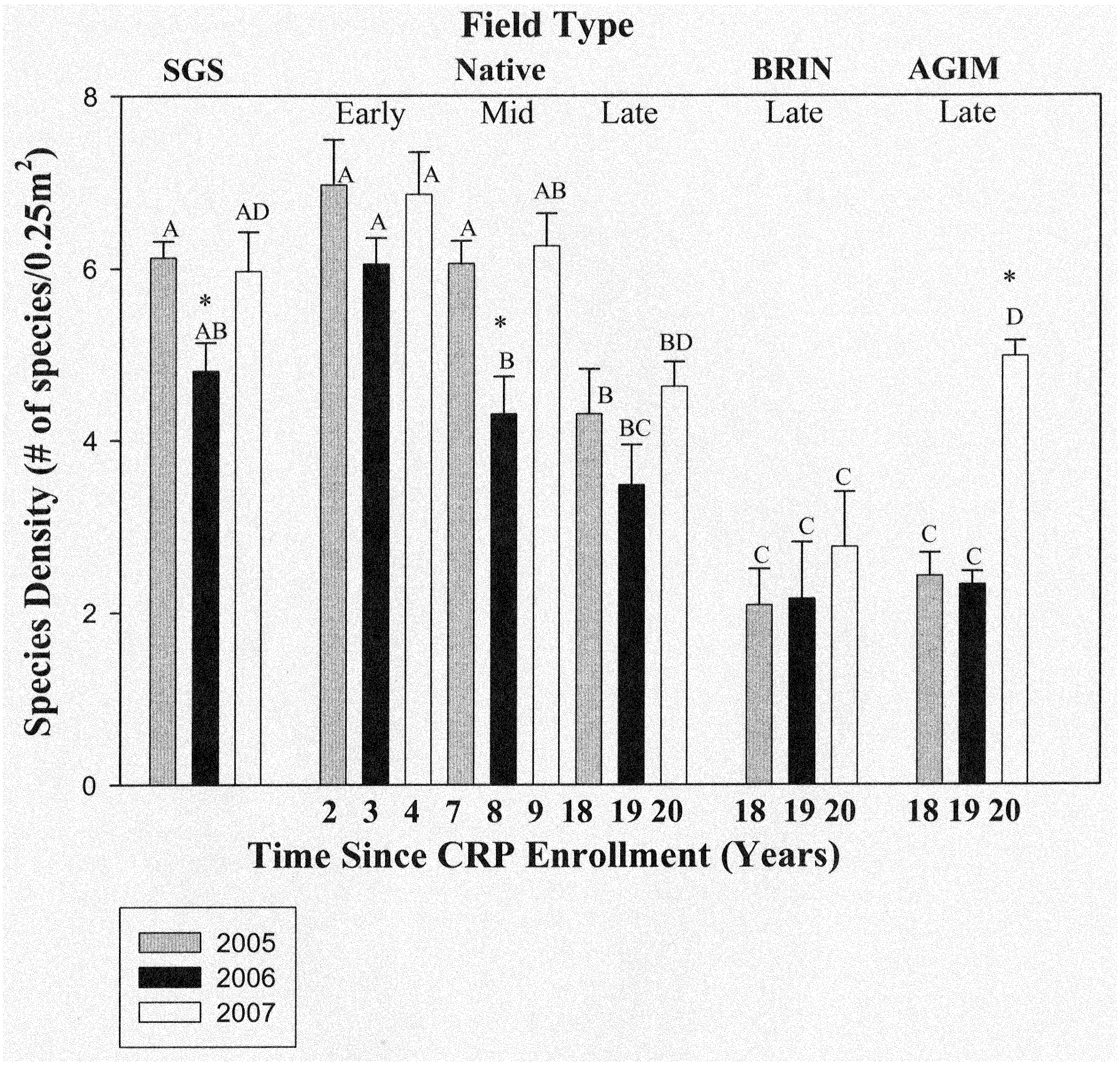

Figure 8. Species density (# of species/0.25m^2) in the shortgrass steppe (SGS) and in relation to time since CRP enrollment in the chronosequence of CRP fields seeded with native perennial grasses (Native - Early, Mid, and Late), and CRP fields seeded with introduced grasses: *Bromus inermis* (BRIN - Late) and *Agropyron intermedium* (AGIN - Late), from 2005-2007. Different capital letters designate significant differences (Tukey adjusted $P < 0.05$) in species density among field types within the same sampling year. An asterisk (*) designates a significant (Tukey adjusted $P < 0.05$) interannual difference in species density from the other two sampling years within the same field type.

Appendix A. Relative percent canopy cover of species composition in CRP fields and shortgrass steppe in 2005, 2006, and 2007.

Time Since CRP Enrollment (Years)	**Year Sampled**	**Field Type**	**Species**	**% Relative Canopy Cover**
2	2005	Native-Early	*Helianthus petiolaris*	34.63
2	2005	Native-Early	*Triticum aestivum*	12.56
2	2005	Native-Early	*Salsola iberica*	10.57
2	2005	Native-Early	*Lygodesmia juncea*	8.33
2	2005	Native-Early	*Polygonum aviculare*	8.23
2	2005	Native-Early	*Munroa squarrosa*	5.85
2	2005	Native-Early	*Ipomopsis laxiflora*	3.70
2	2005	Native-Early	*Oenothera albicaulis*	2.62
2	2005	Native-Early	*Panicum capillare*	2.52
2	2005	Native-Early	*Chenopodium leptophyllum*	2.01
2	2005	Native-Early	*Euphorbia serpyllifolia*	1.88
2	2005	Native-Early	*Descurania pinnata*	1.81
2	2005	Native-Early	*Tragopogon dubius*	0.99
2	2005	Native-Early	*Bromus tectorum*	0.83
2	2005	Native-Early	*Conyza canadensis*	0.82
2	2005	Native-Early	*Agropyron smithii*	0.66
2	2005	Native-Early	*Lepidium densiflorum*	0.48
2	2005	Native-Early	*Lactuca serriola*	0.43
2	2005	Native-Early	*Cenchrus longispinus*	0.25
2	2005	Native-Early	*Kochia scoparia*	0.19
2	2005	Native-Early	*Eragrostis cilianensis*	0.14
2	2005	Native-Early	*Mirabilis linearis*	0.11
2	2005	Native-Early	*Medicago sativa*	0.09
2	2005	Native-Early	*Dalea purpurea*	0.09
2	2005	Native-Early	*Machaeranthera tanacetifolia*	0.08
2	2005	Native-Early	*Convolvulus arvensis*	0.06
2	2005	Native-Early	*Gutierrezia sarothrae*	0.03
2	2005	Native-Early	*Chenopodium album*	0.02
2	2005	Native-Early	*Portulaca oleracea*	0.02
2	2005	Native-Early	*Sphaeralcea coccinea*	0.02
3	2006	Native-Early	*Helianthus petiolaris*	16.86
3	2006	Native-Early	*Lygodesmia juncea*	13.91
3	2006	Native-Early	*Bromus tectorum*	12.98
3	2006	Native-Early	*Salsola iberica*	12.63
3	2006	Native-Early	*Conyza canadensis*	7.89
3	2006	Native-Early	*Munroa squarrosa*	7.48
3	2006	Native-Early	*Agropyron smithii*	6.31
3	2006	Native-Early	*Bouteloua curtipendula*	3.00
3	2006	Native-Early	*Triticum aestivum*	2.48

3	2006	Native-Early	*Polygonum aviculare*		2.05
3	2006	Native-Early	*Bouteloua gracilis*		1.98
3	2006	Native-Early	*Portulaca oleracea*		1.94
3	2006	Native-Early	*Descurania pinnata*		1.69
3	2006	Native-Early	*Tragopogon dubius*		1.61
3	2006	Native-Early	*Euphorbia serpyllifolia*		1.25
3	2006	Native-Early	*Ipomopsis laxiflora*		1.15
3	2006	Native-Early	*Chenopodium leptophyllum*		0.84
3	2006	Native-Early	*Panicum capillare*		0.74
3	2006	Native-Early	*Lepidium densiflorum*		0.55
3	2006	Native-Early	*Oenothera albicaulis*		0.41
3	2006	Native-Early	*Cenchrus longispinus*		0.33
3	2006	Native-Early	*Chrysopsis villosa*		0.33
3	2006	Native-Early	*Cirsium arvense*		0.33
3	2006	Native-Early	*Eragrostis cilianensis*		0.24
3	2006	Native-Early	*Dalea purpurea*		0.21
3	2006	Native-Early	*Medicago sativa*		0.21
3	2006	Native-Early	*Convolvulus arvensis*		0.13
3	2006	Native-Early	*Kochia scoparia*		0.11
3	2006	Native-Early	*Chenopodium album*		0.09
3	2006	Native-Early	*Lactuca serriola*		0.09
3	2006	Native-Early	*Machaeranthera tanacetifolia*		0.09
3	2006	Native-Early	Unknown forb		0.03
3	2006	Native-Early	*Aristida purpurea*		0.02
3	2006	Native-Early	*Plantago patagonica*		0.02
3	2006	Native-Early	Unknown forb		0.02
4	2007	Native-Early	*Bromus tectorum*		22.40
4	2007	Native-Early	*Salsola iberica*		19.79
4	2007	Native-Early	*Helianthus petiolaris*		8.59
4	2007	Native-Early	*Agropyron smithii*		8.22
4	2007	Native-Early	*Bouteloua curtipendula*		7.21
4	2007	Native-Early	*Euphorbia serpyllifolia*		6.28
4	2007	Native-Early	*Portulaca oleracea*		5.14
4	2007	Native-Early	*Eragrostis cilianensis*		4.97
4	2007	Native-Early	*Bouteloua gracilis*		4.58
4	2007	Native-Early	*Lygodesmia juncea*		2.54
4	2007	Native-Early	*Munroa squarrosa*		2.10
4	2007	Native-Early	*Chenopodium leptophyllum*		1.94
4	2007	Native-Early	*Panicum capillare*		1.47
4	2007	Native-Early	*Oenothera albicaulis*		0.94
4	2007	Native-Early	*Stipa viridula*		0.89
4	2007	Native-Early	*Polygonum aviculare*		0.66
4	2007	Native-Early	*Ratibida columnifera*		0.29
4	2007	Native-Early	*Descurania pinnata*		0.27
4	2007	Native-Early	Unknown forb		0.27
4	2007	Native-Early	*Ambrosia psilostachya*		0.22
4	2007	Native-Early	*Tragopogon dubius*		0.22

4	2007	Native-Early	*Kochia scoparia*		0.18
4	2007	Native-Early	*Convolvulus arvensis*		0.13
4	2007	Native-Early	*Chenopodium incanum*		0.12
4	2007	Native-Early	*Cenchrus longispinus*		0.10
4	2007	Native-Early	*Medicago sativa*		0.08
4	2007	Native-Early	*Ipomopsis laxiflora*		0.08
4	2007	Native-Early	*Lepidium densiflorum*		0.07
4	2007	Native-Early	*Amaranthus retroflexus*		0.05
4	2007	Native-Early	*Chrysopsis villosa*		0.05
4	2007	Native-Early	*Erigeron flagellaris*		0.05
4	2007	Native-Early	*Sphaeralcea coccinea*		0.05
4	2007	Native-Early	*Oxytropis lambertii*		0.03
4	2007	Native-Early	*Aristida purpurea*		0.01
4	2007	Native-Early	*Plantago patagonica*		0.01
7	2005	Native-Mid	*Bromus tectorum*		64.62
7	2005	Native-Mid	*Tragopogon dubius*		7.63
7	2005	Native-Mid	*Agropyron smithii*		5.73
7	2005	Native-Mid	*Bouteloua curtipendula*		4.85
7	2005	Native-Mid	*Sitanion hystrix*		2.59
7	2005	Native-Mid	*Stipa viridula*		2.41
7	2005	Native-Mid	*Salsola iberica*		2.04
7	2005	Native-Mid	*Medicago sativa*		1.83
7	2005	Native-Mid	*Conyza canadensis*		1.81
7	2005	Native-Mid	*Chrysopsis villosa*		1.15
7	2005	Native-Mid	*Euphorbia serpyllifolia*		1.09
7	2005	Native-Mid	*Aristida purpurea*		0.75
7	2005	Native-Mid	*Bouteloua gracilis*		0.68
7	2005	Native-Mid	*Eragrostis cilianensis*		0.67
7	2005	Native-Mid	*Panicum virgatum*		0.59
7	2005	Native-Mid	*Convolvulus arvensis*		0.42
7	2005	Native-Mid	*Lactuca serriola*		0.30
7	2005	Native-Mid	*Kochia scoparia*		0.24
7	2005	Native-Mid	*Descurania pinnata*		0.19
7	2005	Native-Mid	*Sphaeralcea coccinea*		0.15
7	2005	Native-Mid	*Portulaca oleracea*		0.08
7	2005	Native-Mid	Unknown forb		0.05
7	2005	Native-Mid	*Ambrosia psilostachya*		0.04
7	2005	Native-Mid	*Taraxacum offininale*		0.04
7	2005	Native-Mid	*Helianthus petiolaris*		0.02
7	2005	Native-Mid	*Chenopodium leptophyllum*		0.01
7	2005	Native-Mid	*Machaeranthera tanacetifolia*		0.01
7	2005	Native-Mid	*Oenothera albicaulis*		0.01
8	2006	Native-Mid	*Bromus tectorum*		51.01
8	2006	Native-Mid	*Agropyron smithii*		9.77
8	2006	Native-Mid	*Bouteloua curtipendula*		8.25
8	2006	Native-Mid	*Sitanion hystrix*		7.51

8	2006	Native-Mid	*Stipa viridula*	5.36
8	2006	Native-Mid	*Chrysopsis villosa*	3.87
8	2006	Native-Mid	*Tragopogon dubius*	3.26
8	2006	Native-Mid	*Aristida purpurea*	2.82
8	2006	Native-Mid	*Salsola iberica*	2.65
8	2006	Native-Mid	*Bouteloua gracilis*	1.52
8	2006	Native-Mid	*Medicago sativa*	1.13
8	2006	Native-Mid	*Portulaca oleracea*	0.69
8	2006	Native-Mid	*Euphorbia serpyllifolia*	0.63
8	2006	Native-Mid	*Sporobolus cryptandrus*	0.49
8	2006	Native-Mid	*Cenchrus longispinus*	0.24
8	2006	Native-Mid	*Cirsium arvense*	0.24
8	2006	Native-Mid	*Sorghastrum nutans*	0.24
8	2006	Native-Mid	*Sphaeralcea coccinea*	0.21
8	2006	Native-Mid	*Descurania pinnata*	0.07
8	2006	Native-Mid	*Ambrosia psilostachya*	0.01
8	2006	Native-Mid	*Oenothera albicaulis*	0.01
8	2006	Native-Mid	Unknown forb	0.01
9	2007	Native-Mid	*Bromus tectorum*	36.00
9	2007	Native-Mid	*Salsola iberica*	27.22
9	2007	Native-Mid	*Agropyron smithii*	5.41
9	2007	Native-Mid	*Stipa viridula*	4.54
9	2007	Native-Mid	*Portulaca oleracea*	4.44
9	2007	Native-Mid	*Euphorbia serpyllifolia*	4.16
9	2007	Native-Mid	*Aristida purpurea*	2.71
9	2007	Native-Mid	*Eragrostis cilianensis*	2.68
9	2007	Native-Mid	*Bouteloua curtipendula*	2.38
9	2007	Native-Mid	*Chrysopsis villosa*	1.76
9	2007	Native-Mid	*Convolvulus arvensis*	1.55
9	2007	Native-Mid	*Chenopodium album*	1.45
9	2007	Native-Mid	*Medicago sativa*	1.39
9	2007	Native-Mid	*Tragopogon dubius*	0.84
9	2007	Native-Mid	*Sitanion hystrix*	0.78
9	2007	Native-Mid	*Oenothera albicaulis*	0.70
9	2007	Native-Mid	*Bouteloua gracilis*	0.52
9	2007	Native-Mid	*Kochia scoparia*	0.28
9	2007	Native-Mid	*Sporobolus cryptandrus*	0.27
9	2007	Native-Mid	*Amaranthus retroflexus*	0.25
9	2007	Native-Mid	*Bromus inermis*	0.24
9	2007	Native-Mid	*Chenopodium leptophyllum*	0.13
9	2007	Native-Mid	*Panicum capillare*	0.12
9	2007	Native-Mid	*Sphaeralcea coccinea*	0.05
9	2007	Native-Mid	*Lepidium densiflorum*	0.04
9	2007	Native-Mid	*Chenopodium incanum*	0.04
9	2007	Native-Mid	*Descurania pinnata*	0.04
9	2007	Native-Mid	*Ambrosia psilostachya*	0.01
9	2007	Native-Mid	*Crytantha crassisepala*	0.01

9	2007	Native-Mid	*Helianthus petiolaris*	0.01
9	2007	Native-Mid	*Lappula redowskii*	0.01
18	2005	Native-Late	*Agropyron smithii*	35.98
18	2005	Native-Late	*Bouteloua curtipendula*	27.76
18	2005	Native-Late	*Bouteloua gracilis*	17.75
18	2005	Native-Late	*Sporobolus cryptandrus*	5.57
18	2005	Native-Late	*Aristida purpurea*	4.32
18	2005	Native-Late	*Salsola iberica*	1.04
18	2005	Native-Late	*Chrysopsis villosa*	0.89
18	2005	Native-Late	*Gutierrezia sarothrae*	0.76
18	2005	Native-Late	*Kochia scoparia*	0.66
18	2005	Native-Late	*Sphaeralcea coccinea*	0.66
18	2005	Native-Late	*Schizachyrium scoparium*	0.60
18	2005	Native-Late	*Plantago patagonica*	0.58
18	2005	Native-Late	*Oenothera albicaulis*	0.54
18	2005	Native-Late	*Vulpia octoflora*	0.53
18	2005	Native-Late	*Artemisia frigida*	0.46
18	2005	Native-Late	*Descurania pinnata*	0.34
18	2005	Native-Late	*Lepidium densiflorum*	0.29
18	2005	Native-Late	*Machaeranthera tanacetifolia*	0.25
18	2005	Native-Late	*Euphorbia serpyllifolia*	0.19
18	2005	Native-Late	*Portulaca oleracea*	0.19
18	2005	Native-Late	*Chenopodium leptophyllum*	0.17
18	2005	Native-Late	*Schedonnardis paniculatus*	0.15
18	2005	Native-Late	*Agropyron cristatum*	0.08
18	2005	Native-Late	*Conyza canadensis*	0.07
18	2005	Native-Late	*Lygodesmia juncea*	0.07
18	2005	Native-Late	*Medicago sativa*	0.06
18	2005	Native-Late	*Convolvulus arvensis*	0.02
18	2005	Native-Late	*Bromus tectorum*	0.01
18	2005	Native-Late	*Echinocereus viridiflorus*	0.01
19	2006	Native-Late	*Bouteloua curtipendula*	27.96
19	2006	Native-Late	*Agropyron smithii*	26.54
19	2006	Native-Late	*Bouteloua gracilis*	15.58
19	2006	Native-Late	*Sporobolus cryptandrus*	12.21
19	2006	Native-Late	*Aristida purpurea*	5.76
19	2006	Native-Late	*Portulaca oleracea*	5.33
19	2006	Native-Late	*Agropyron cristatum*	1.48
19	2006	Native-Late	*Chrysopsis villosa*	1.41
19	2006	Native-Late	*Oenothera albicaulis*	0.70
19	2006	Native-Late	*Bromus inermis*	0.69
19	2006	Native-Late	*Sphaeralcea coccinea*	0.53
19	2006	Native-Late	*Salsola iberica*	0.36
19	2006	Native-Late	*Kochia scoparia*	0.24
19	2006	Native-Late	*Plantago patagonica*	0.23
19	2006	Native-Late	*Lepidium densiflorum*	0.21

19	2006	Native-Late	*Vulpia octoflora*	0.21
19	2006	Native-Late	*Euphorbia serpyllifolia*	0.20
19	2006	Native-Late	*Artemisia frigida*	0.13
19	2006	Native-Late	*Chenopodium leptophyllum*	0.06
19	2006	Native-Late	*Descurania pinnata*	0.06
19	2006	Native-Late	*Gutierrezia sarothrae*	0.06
19	2006	Native-Late	*Bromus tectorum*	0.01
19	2006	Native-Late	*Machaeranthera tanacetifolia*	0.01
20	2007	Native-Late	*Bouteloua curtipendula*	23.14
20	2007	Native-Late	*Bouteloua gracilis*	16.80
20	2007	Native-Late	*Sporobolus cryptandrus*	15.48
20	2007	Native-Late	*Agropyron smithii*	12.37
20	2007	Native-Late	*Aristida purpurea*	9.34
20	2007	Native-Late	*Salsola iberica*	5.42
20	2007	Native-Late	*Portulaca oleracea*	4.04
20	2007	Native-Late	*Kochia scoparia*	3.34
20	2007	Native-Late	*Chenopodium leptophyllum*	3.21
20	2007	Native-Late	*Chrysopsis villosa*	1.16
20	2007	Native-Late	*Schedonnardis paniculatus*	0.78
20	2007	Native-Late	*Plantago patagonica*	0.71
20	2007	Native-Late	*Sphaeralcea coccinea*	0.58
20	2007	Native-Late	*Lepidium densiflorum*	0.48
20	2007	Native-Late	*Euphorbia serpyllifolia*	0.46
20	2007	Native-Late	*Gutierrezia sarothrae*	0.43
20	2007	Native-Late	*Artemisia frigida*	0.37
20	2007	Native-Late	*Convolvulus arvensis*	0.35
20	2007	Native-Late	*Opuntia polyacantha*	0.35
20	2007	Native-Late	*Medicago sativa*	0.34
20	2007	Native-Late	*Chenopodium incanum*	0.28
20	2007	Native-Late	*Lygodesmia juncea*	0.23
20	2007	Native-Late	*Agropyron cristatum*	0.10
20	2007	Native-Late	*Munroa squarrosa*	0.07
20	2007	Native-Late	*Oenothera albicaulis*	0.07
20	2007	Native-Late	*Talinum parviflorum*	0.06
20	2007	Native-Late	*Ambrosia psilostachya*	0.01
20	2007	Native-Late	*Descurania pinnata*	0.01
20	2007	Native-Late	*Eragrostis cilianensis*	0.01
20	2007	Native-Late	*Ipomopsis laxiflora*	0.01
18	2005	BRIN-Late	*Bromus inermis*	80.76
18	2005	BRIN-Late	*Chrysopsis villosa*	7.07
18	2005	BRIN-Late	*Aristida purpurea*	5.56
18	2005	BRIN-Late	*Sporobolus cryptandrus*	1.74
18	2005	BRIN-Late	*Salsola iberica*	1.44
18	2005	BRIN-Late	*Agropyron intermedium*	1.39
18	2005	BRIN-Late	*Cirsium arvense*	0.93
18	2005	BRIN-Late	*Convolvulus arvensis*	0.32

18	2005	BRIN-Late	*Sphaeralcea coccinea*	0.23
18	2005	BRIN-Late	*Lygodesmia juncea*	0.19
18	2005	BRIN-Late	*Erigeron flagellaris*	0.14
18	2005	BRIN-Late	*Agropyron smithii*	0.14
18	2005	BRIN-Late	*Medicago sativa*	0.05
18	2005	BRIN-Late	*Kochia scoparia*	0.02
18	2005	BRIN-Late	*Plantago patagonica*	0.02
19	2006	BRIN-Late	*Bromus inermis*	63.70
19	2006	BRIN-Late	*Sporobolus cryptandrus*	14.68
19	2006	BRIN-Late	*Aristida purpurea*	11.35
19	2006	BRIN-Late	*Chrysopsis villosa*	5.53
19	2006	BRIN-Late	*Portulaca oleracea*	2.78
19	2006	BRIN-Late	*Convolvulus arvensis*	1.04
19	2006	BRIN-Late	*Salsola iberica*	0.43
19	2006	BRIN-Late	*Sphaeralcea coccinea*	0.23
19	2006	BRIN-Late	*Lygodesmia juncea*	0.10
19	2006	BRIN-Late	*Euphorbia serpyllifolia*	0.07
19	2006	BRIN-Late	*Munroa squarrosa*	0.05
19	2006	BRIN-Late	*Agropyron intermedium*	0.02
19	2006	BRIN-Late	*Medicago sativa*	0.02
20	2007	BRIN-Late	*Bromus inermis*	58.81
20	2007	BRIN-Late	*Sporobolus cryptandrus*	17.80
20	2007	BRIN-Late	*Aristida purpurea*	11.60
20	2007	BRIN-Late	*Chrysopsis villosa*	4.10
20	2007	BRIN-Late	*Portulaca oleracea*	3.85
20	2007	BRIN-Late	*Euphorbia serpyllifolia*	1.52
20	2007	BRIN-Late	*Salsola iberica*	1.14
20	2007	BRIN-Late	*Convolvulus arvensis*	0.81
20	2007	BRIN-Late	*Cenchrus longispinus*	0.11
20	2007	BRIN-Late	*Munroa squarrosa*	0.11
20	2007	BRIN-Late	*Oenothera albicaulis*	0.11
20	2007	BRIN-Late	*Plantago patagonica*	0.04
20	2007	BRIN-Late	*Polygonum aviculare*	0.02
18	2005	AGIN-Late	*Agropyron intermedium*	72.87
18	2005	AGIN-Late	*Aristida purpurea*	15.46
18	2005	AGIN-Late	*Chrysopsis villosa*	5.17
18	2005	AGIN-Late	*Sporobolus cryptandrus*	1.21
18	2005	AGIN-Late	*Tragopogon dubius*	1.02
18	2005	AGIN-Late	*Cirsium arvense*	0.98
18	2005	AGIN-Late	*Bromus inermis*	0.62
18	2005	AGIN-Late	*Sphaeralcea coccinea*	0.52
18	2005	AGIN-Late	*Salsola iberica*	0.50
18	2005	AGIN-Late	*Lepidium densiflorum*	0.45
18	2005	AGIN-Late	*Lactuca serriola*	0.33
18	2005	AGIN-Late	*Kochia scoparia*	0.29

18	2005	AGIN-Late	*Plantago patagonica*	0.21
18	2005	AGIN-Late	*Conyza canadensis*	0.17
18	2005	AGIN-Late	*Bromus tectorum*	0.14
18	2005	AGIN-Late	*Helianthus petiolaris*	0.02
18	2005	AGIN-Late	Unknown forb	0.02
19	2006	AGIN-Late	*Agropyron intermedium*	78.61
19	2006	AGIN-Late	*Aristida purpurea*	11.73
19	2006	AGIN-Late	*Sporobolus cryptandrus*	3.54
19	2006	AGIN-Late	*Portulaca oleracea*	3.25
19	2006	AGIN-Late	*Bromus inermis*	1.16
19	2006	AGIN-Late	*Chrysopsis villosa*	0.68
19	2006	AGIN-Late	*Tragopogon dubius*	0.64
19	2006	AGIN-Late	*Plantago patagonica*	0.20
19	2006	AGIN-Late	*Sphaeralcea coccinea*	0.12
19	2006	AGIN-Late	*Salsola iberica*	0.06
19	2006	AGIN-Late	*Euphorbia serpyllifolia*	0.01
19	2006	AGIN-Late	*Kochia scoparia*	0.01
20	2007	AGIN-Late	*Agropyron intermedium*	28.85
20	2007	AGIN-Late	*Salsola iberica*	16.80
20	2007	AGIN-Late	*Portulaca oleracea*	15.49
20	2007	AGIN-Late	*Aristida purpurea*	14.42
20	2007	AGIN-Late	*Sporobolus cryptandrus*	11.13
20	2007	AGIN-Late	*Chenopodium album*	4.23
20	2007	AGIN-Late	*Euphorbia serpyllifolia*	3.00
20	2007	AGIN-Late	*Kochia scoparia*	1.93
20	2007	AGIN-Late	*Convolvulus arvensis*	0.80
20	2007	AGIN-Late	*Chrysopsis villosa*	0.61
20	2007	AGIN-Late	*Plantago patagonica*	0.55
20	2007	AGIN-Late	*Amaranthus retroflexus*	0.51
20	2007	AGIN-Late	*Tragopogon dubius*	0.51
20	2007	AGIN-Late	*Lepidium densiflorum*	0.45
20	2007	AGIN-Late	*Sphaeralcea coccinea*	0.28
20	2007	AGIN-Late	*Bromus tectorum*	0.27
20	2007	AGIN-Late	*Bromus inermis*	0.06
20	2007	AGIN-Late	*Descurania pinnata*	0.06
20	2007	AGIN-Late	*Lygodesmia juncea*	0.06
	2005	SGS	*Bouteloua gracilis*	49.35
	2005	SGS	*Buchloe dactyloides*	23.45
	2005	SGS	*Carex eleocharis*	6.51
	2005	SGS	*Vulpia octoflora*	5.64
	2005	SGS	*Aristida purpurea*	2.28
	2005	SGS	*Sphaeralcea coccinea*	2.09
	2005	SGS	*Thelesperma filifolium*	1.63
	2005	SGS	*Stipa comata*	1.22
	2005	SGS	*Opuntia polyacantha*	1.17

	2005	SGS	*Gutierrezia sarothrae*	1.09
	2005	SGS	*Agropyron smithii*	0.99
	2005	SGS	*Eriogonum effusum*	0.93
	2005	SGS	*Astragulus missouriensis*	0.73
	2005	SGS	*Sporobolus cryptandrus*	0.71
	2005	SGS	*Crytantha crassisepala*	0.56
	2005	SGS	*Sitanion hystrix*	0.36
	2005	SGS	*Artemisia frigida*	0.19
	2005	SGS	*Plantago patagonica*	0.17
	2005	SGS	*Oenothera albicaulis*	0.14
	2005	SGS	*Mirabilis linearis*	0.11
	2005	SGS	*Machaeranthera tanacetifolia*	0.10
	2005	SGS	*Psoralea tenuiflora*	0.10
	2005	SGS	*Lepidium densiflorum*	0.09
	2005	SGS	*Chenopodium leptophyllum*	0.09
	2005	SGS	*Echinocereus viridiflorus*	0.09
	2005	SGS	*Lygodesmia juncea*	0.09
	2005	SGS	*Muhlenbergia torreyi*	0.04
	2005	SGS	*Triticum aestivum*	0.04
	2005	SGS	*Chrysopsis villosa*	0.01
	2005	SGS	*Iva xanthifolia*	0.01
	2005	SGS	*Penstemon angustifolius*	0.01
	2005	SGS	*Picradeniopsis oppositifolia*	0.01
	2005	SGS	Unknown forb	0.01
	2006	SGS	*Bouteloua gracilis*	57.47
	2006	SGS	*Buchloe dactyloides*	16.22
	2006	SGS	*Carex eleocharis*	10.98
	2006	SGS	*Opuntia polyacantha*	2.90
	2006	SGS	*Sporobolus cryptandrus*	2.17
	2006	SGS	*Vulpia octoflora*	2.03
	2006	SGS	*Sphaeralcea coccinea*	1.98
	2006	SGS	*Aristida purpurea*	1.70
	2006	SGS	*Gutierrezia sarothrae*	1.11
	2006	SGS	*Eriogonum effusum*	0.78
	2006	SGS	*Agropyron smithii*	0.75
	2006	SGS	*Sitanion hystrix*	0.61
	2006	SGS	*Artemisia frigida*	0.31
	2006	SGS	*Stipa comata*	0.24
	2006	SGS	*Lygodesmia juncea*	0.18
	2006	SGS	*Chrysothamnus nauseosus*	0.13
	2006	SGS	*Echinocereus viridiflorus*	0.12
	2006	SGS	*Psoralea tenuiflora*	0.09
	2006	SGS	*Oxytropis lambertii*	0.06
	2006	SGS	*Euphorbia serpyllifolia*	0.04
	2006	SGS	*Muhlenbergia torreyi*	0.04
	2006	SGS	Unknown forb	0.04
	2006	SGS	Unknown forb	0.03

	2006	SGS	*Thelesperma filifolium*	0.01
	2006	SGS	*Chrysopsis villosa*	0.01
	2007	SGS	*Bouteloua gracilis*	53.86
	2007	SGS	*Buchloe dactyloides*	16.77
	2007	SGS	*Carex eleocharis*	9.82
	2007	SGS	*Sphaeralcea coccinea*	2.99
	2007	SGS	*Sporobolus cryptandrus*	2.89
	2007	SGS	*Opuntia polyacantha*	2.52
	2007	SGS	*Vulpia octoflora*	1.89
	2007	SGS	*Aristida purpurea*	1.67
	2007	SGS	*Oxytropis lambertii*	1.35
	2007	SGS	*Thelesperma filifolium*	1.08
	2007	SGS	*Eriogonum effusum*	0.90
	2007	SGS	*Artemisia frigida*	0.62
	2007	SGS	*Echinocereus viridiflorus*	0.49
	2007	SGS	*Agropyron smithii*	0.39
	2007	SGS	*Gutierrezia sarothrae*	0.36
	2007	SGS	*Mirabilis linearis*	0.35
	2007	SGS	*Sitanion hystrix*	0.34
	2007	SGS	*Euphorbia serpyllifolia*	0.29
	2007	SGS	*Crytantha crassisepala*	0.25
	2007	SGS	*Stipa comata*	0.19
	2007	SGS	*Chrysopsis villosa*	0.12
	2007	SGS	*Picradeniopsis oppositifolia*	0.10
	2007	SGS	*Plantago patagonica*	0.10
	2007	SGS	*Psoralea tenuiflora*	0.10
	2007	SGS	*Lepidium densiflorum*	0.09
	2007	SGS	*Chenopodium leptophyllum*	0.08
	2007	SGS	*Machaeranthera tanacetifolia*	0.08
	2007	SGS	*Lappula redowskii*	0.08
	2007	SGS	*Gaura coccinea*	0.04
	2007	SGS	*Lygodesmia juncea*	0.04
	2007	SGS	*Portulaca oleracea*	0.04
	2007	SGS	*Astragulus mollissimus*	0.03
	2007	SGS	*Iva xanthifolia*	0.03
	2007	SGS	*Allium geyeri*	0.01
	2007	SGS	*Chenopodium incanum*	0.01

Chapter 3. Vegetation Structure and Net Primary Production on Conservation Reserve Program Lands in Northeastern Colorado

Introduction

Physical and biotic factors constrain vegetation structure and its influence on ecosystem function (Grime 1977). Disturbance can push these factors outside the range of natural variability (Pickett and White 1985) and facilitate species with a growth form and allocation strategy that are adapted to the altered physical and biotic environment (Grime 1979, Bazzaz 1983, Tilman 1988, Smith and Huston 1989). Following disturbance, this environment is dynamic and influences vegetation structure by selecting species with suitable traits out of a species pool (Woodward and Diament 1991, Keddy 1992) during the course of succession and affects the growth of these species at shorter time scales (Sims and Singh 1978a). Understanding how vegetation structure changes is important because it can affect ecosystem properties, including net primary production (NPP; Lieth and Whittaker 1975, Lauenroth and Sala 1992, Yahdjian and Sala 2006). Recognizing disturbance characteristics (Sousa 1984) and factors that influence vegetation structure and NPP following disturbance is critical for understanding the recovery of ecosystem function (Chapin et al. 2000, Lavorel and Garnier 2002).

Dryland (non-irrigated) wheat cropping is a large scale disturbance in the shortgrass steppe (Lauenroth and Milchunas 1992) that encompassed 1 million hectares of harvested land in Colorado in 2007 (USDA National Agricultural Statistics Service 2008). This land use destroys above and belowground components of a diverse plant community and replaces them with an annually harvested crop. It also alters the physical and chemical characteristics of the soil (Burke et al. 1989), which influences vegetation recovery. Abandonment of cultivated fields initiates the process of succession as vegetation structure and associated ecosystem properties recover from the impacts of tillage and crop production practices. Land management practices can influence the recovery process. The USDA Conservation Reserve Program (CRP) has converted cultivated land to perennial vegetation and currently includes an area equivalent to the 2007 wheat harvest in Colorado (USDA Farm Service Agency 2008). CRP land in this region is seeded with a variety of seed mixes that contain perennial grasses to meet management objectives, including reduction in soil erosion and improvement of water quality (Skold 1989).

Time since CRP enrollment and seed mix are important factors that constrain the species pool, thereby influencing plant community composition (Chapter 2). Early CRP fields (2-4 years after enrollment) are composed of a species rich forb and annual grass community, likely determined by the environment, seedbank, and stochastic dispersal events from nearby fields (Egler 1954, Coffin and Lauenroth 1989, Coffin et al. 1996). An increase of perennial grass canopy cover is relatively slow and variable during this period, but within 18 years perennial grasses in the seed mix dominate the plant community with low species richness. Many of these perennial grasses are introduced species and varieties not native to the northern shortgrass steppe.

Vegetation structure is indirectly influenced by time since CRP enrollment and seed mix through plant community composition. As annual grasses and forbs colonize and grow in early CRP fields, plant basal cover, density, and height are likely to increase. Perennial grass replacement of this early seral stage may increase plant basal cover and height, but reduce plant density. Vegetation structure at the seeded perennial grass stage is likely to be dependent on the species that established from the CRP seed mix. The native seed mix contains mostly mid-height (20-30 cm) caespitose grasses, whereas the introduced seed mix has tall-growing (50+ cm) rhizomatous grasses. The differences in vegetation structure of introduced seeded species have the potential to alter ecosystem properties (Vitousek 1990, Christian and Wilson 1999, Seabloom et al. 2003) relative to native seeded species and undisturbed shortgrass steppe.

Plant community composition and associated vegetation structure are indicative of the potential for plant growth and the allocation of net primary production. Annuals, which have the potential to occur at high density in early CRP fields, can grow rapidly and respond quickly to environmental change (Lauenroth et al. 1978). This can result in relatively high aboveground net primary production, low investment in belowground net primary production due to an ephemeral root system, and high interannual variability in total net primary production due to a rapid growth response when environmental conditions are favorable. The perennial grasses that establish in CRP fields may allocate production differently than perennial grasses in undisturbed shortgrass steppe. *Bouteloua gracilis*, the dominant perennial bunchgrass in the shortgrass steppe, has a relatively low aboveground to belowground production ratio (Milchunas and Lauenroth 2001), which makes it resistant to grazing and drought. In contrast, CRP fields are seeded with many perennial grass species and varieties that are native to regions with greater water availability, where light is a more limiting factor in plant growth (Lauenroth and Coffin 1992). This may cause an increase in allocation to aboveground photosynthetic tissue and less allocation belowground. Furthermore, many CRP planted species (*Agropyron* spp.) are known to have high aboveground production and low root:shoot ratios (Redente et al. 1989). Potential differences in vegetation structure, such as height and basal cover, between fields seeded with native and introduced seed mixes may lead to differences in NPP at the individual plant and field scale.

Resource availability can constrain vegetation structure and net primary production (NPP) directly or indirectly through its effect on plant community composition. Low mean annual precipitation in the shortgrass steppe (Lauenroth and Sala 1992) can limit the species in the plant community and their respective structures and contribution to NPP in the long-term (MacMahon 1980). The vegetation structure and allocation strategy of plants that persist in CRP fields can provide further insight on what vegetation characteristics are adaptive to this region. At a shorter time scale, high variability in annual precipitation in this region (Lauenroth and Sala 1992) can result in fluctuations in vegetation structure and NPP determined by the growth responses of species in the field. Understanding how vegetation structure and NPP change with interannual variability in the timing and amount of precipitation may explain the plasticity of plant growth in this region.

My objective is to determine the vegetation structure and net primary production in CRP fields relative to undisturbed shortgrass steppe, and the influence physical and biotic factors have in explaining variability in these vegetation characteristics. Specifically, I addressed the following questions:

1) How does time since CRP enrollment and seed mix affect vegetation structure and NPP through its influence on species composition in CRP plant communities?

2) What is the interannual variability of vegetation structure and NPP and is it affected by annual precipitation?

3) How does vegetation structure and NPP in CRP fields compare to undisturbed shortgrass steppe?

Methods

Study sites

I 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 northeast 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 semiarid with a long-term mean annual precipitation (1969-2007) of 332 mm ($\sigma = 99$ mm), 80% of which falls between April and September, and a mean annual temperature of 9.6°C ($\sigma = 1.1$°C). Undisturbed shortgrass steppe is codominated by the C_4 perennial grasses *Bouteloua gracilis*[*] and *Buchloë dactyloides* (Chapter 2). Other important functional types included C_3 graminoids, forbs, dwarf shrubs, and prickly pear cactus. My shortgrass steppe sites had been long-term moderately summer grazed, but I excluded them from grazing during the study.

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[*] plant nomenclature follows Great Plains Flora Association 1986

I partitioned CRP sites into those seeded with perennial grasses 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), *Bouteloua 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 time since CRP enrollment, I established a chronosequence (Stevens and Walker 1970), which consisted of three field age classes: early, mid, and late. All fields in the chronosequence were seeded with a native seed mix to minimize differences in the potential vegetation. I sampled each field for 3 years to account for environmental variability. Early fields represented 2-4 years after CRP enrollment, mid fields represented 7-9 years after CRP enrollment, and late fields represented 18-20 years after CRP enrollment. To address differences in seed mix, I 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 three year study.

All fields were in a non-irrigated wheat-fallow rotation prior to CRP enrollment. The year of CRP enrollment, 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 (~ 0.5 g m^{-2} seed) 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 a similar topographic relief (< 3% slope). I replicated each of the six field types three times for a total of eighteen fields sampled (6 field types x 3 field replicates = 18 fields sampled).

Sampling Methods

I measured maximum plant height by species, plant density, and plant basal cover in 40 ¼ m^2 circular quadrats (spaced 20 m apart) in each field in late August/early September 2005, 2006, and 2007. Average maximum plant height of all species was used to represent the composite height of all plants in the quadrat. For clonal species, an individual plant was defined as a group of tillers connected by a crown (Coffin and Lauenroth 1988, Fair et al. 1999).

I estimated aboveground net primary production (ANPP) by species (except cactus species) in 8 of the quadrats (spaced 40 m apart) by clipping aboveground biomass at the soil surface, sorting out dead biomass from previous growing seasons, and weighing after drying at 55°C for 48 hours. Standing and detached dead biomass were collected, dried, and weighed in each of the 8 quadrats as an estimate of litter biomass. Because of the early senescence of *Bromus tectorum*, an introduced winter annual grass, I estimated height, density, basal cover, and ANPP in early June and incorporated these into the field estimates.

To determine belowground biomass, I removed eight soil cores (5 cm in diameter and 30 cm in depth) in early May directly under the dominant perennial grass and eight cores were removed from an adjacent plant interspace (10 cm away from nearest plant) in each field. This sampling stratification was done to encompass spatial variation in root biomass (Hook et al. 1994). Sampling was not stratified in early CRP fields because there were no perennial grasses. I 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.

I filled the holes remaining from the biomass cores with root free soil, forming a root ingrowth core to determine belowground net primary production (BNPP; Jordan and Escalante 1980). Root free soil consisted of soil collected from the same field in which the ingrowth cores were installed. I dry sieved the soil through a wire screen with 1mm openings to remove roots and organic debris. I compacted the root free soil in the ingrowth cores with a dowel to recreate the original bulk density of the soil, but could only recreate 80% of the original bulk density. The following late September/early October, I recored the ingrowth cores using a cylinder with slightly smaller dimensions than the first (4.5 cm in diameter and 25 cm in depth) to minimize sampling outside the ingrowth area.

I separated roots from the biomass and ingrowth cores from soil using a hydropneumatic root elutriator (Smucker et al. 1982). Root elutriation consisted of a combination of washing with water pressure (0.3 MPa) and agitating with air pressure (0.3 MPa) in three 5 minute cycles (agitation only, agitation and washing, and washing only), followed by root collection in 1mm mesh screen sieves. Despite my effort to remove debris from root free soil, there was still noticeable debris in the washed samples. I accounted for this in two ways: 1) I hand picked coarse roots (> 3 mm) from all collection years out of the samples and weighed them separately. 2) I washed root free soil samples from 2007 in the hydropneumatic root elutriator to estimate background organic debris that could not be removed by sieving. The background weights of these samples were subtracted from the weights of debris and fine roots in the ingrowth cores to determine fine root weight alone. I ashed all root and debris material in an Isotemp Muffle Furnace (Model 550-126; Fisher Scientific, Pittsburgh, PA, USA) at 550°C to determine ash-free dry weight. I weighted belowground biomass and BNPP measurements taken between and under plants according to the proportional cover of each microsite to determine estimates at the field scale (Vinton and Burke 1995). I multiplied the average value under perennial grasses in each field by the proportional vegetation basal cover, and multiplied the average value for between perennial grasses in each field by the proportional basal cover of bare ground in each field, and summed the two values. I report all belowground estimates at the field scale.

Statistical Analyses

I performed repeated measures analysis of variance on vegetation characteristics (structure and NPP) with field type as the main effect and year as the repeated measure modeled in an autoregressive correlation structure (Proc Mixed, SAS 9.2, SAS Institute Inc. 2002-2008, Cary, NC, USA). I used a Tukey multiple comparison adjustment when comparing field types separately for each year and years separately for each field type (Proc Glimmix, SAS, June 2006 release). When there was a significant year effect, regression was performed (Proc Reg, SAS 9.2) to evaluate the effect of annual precipitation on the vegetation characteristic. Since there were only three years of precipitation data, they were used to explain patterns which occurred across field types rather than make conclusive statements. Belowground biomass was only measured in 2005. Therefore, analysis of variance was performed with field type and depth as main effects. I performed regressions on plant basal cover, height, and density across time since CRP enrollment of all 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. I performed separate regressions to assess the relationships between vegetation characteristics.

Results

Both inter- and intra-annual variability in precipitation was high during the study. Annual precipitation ranged from 301 mm in 2006 to 409 mm in 2007 (Table 1). Early growing season precipitation ranged from 54 mm in 2006 to 202 in 2005. Similarly, late growing season precipitation was 53 mm in 2005 and 224 in 2007. Early growing season precipitation in 2005 was 42% above the long-term mean and late growing season precipitation was 57% below the mean. 2006 and 2007 showed the opposite trends, with early growing season precipitation 62% and 42% below the mean and late growing season precipitation 16% and 81% above the mean, respectively.

Plant basal cover increased by 0.89% per year along the chronosequence and was at least twice as high in late CRP fields seeded with native perennial grasses than early and mid CRP fields for all years of the study (Fig. 1). Late CRP fields seeded with native grasses had significantly higher basal cover than late CRP fields seeded with introduced grasses for all years of the study except in 2006, when there was no difference between late fields seeded with native perennial grasses and *Agropyron intermedium*. Undisturbed shortgrass steppe had 1.7-5.3 times more plant basal cover than all CRP fields for all years of the study. There was low interannual variability in basal cover.

The average plant height in the CRP chronosequence increased moderately by 0.20 cm per year as time since CRP enrollment increased (Fig.2). The average plant heights in late CRP fields seeded with *Bromus inermis* and *Agropyron intermedium* were 8.7 and 13 cm higher, respectively, than late CRP fields seeded with a native seed mix in 2005. Seeded perennial grasses had the largest influence on these differences, and when considered alone were 11 and 26 cm higher in late *Bromus inermis* and *Agropyron intermedium* fields, 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 all late CRP fields except late CRP fields seeded with *Bromus inermis* in 2007. Annual precipitation explained over half of the interannual variance in average plant height for fields seeded with native perennial grasses and undisturbed shortgrass steppe ($r^2 = 0.60$, $P < 0.0001$), while early growing season precipitation best explained the interannual variance in average plant height in fields seeded with introduced perennial grasses ($r^2 = 0.71$, $P < 0.0001$).

In contrast to plant basal cover, plant density decreased by 1.5 individuals/year (Fig. 3). Plant density was not significantly different between late CRP fields seeded with native and introduced perennial grasses. However, perennial grass density was lower in late CRP fields seeded with *Agropyron intermedium* compared to the other 18 year CRP fields ($t = 9.1$, $P = 0.01$). 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

Bromus inermis. Interannual variability in plant density was high, especially in early and mid CRP fields. Annual precipitation explained half the variability in these fields ($r^2 = 0.49$, $P = 0.001$).

Aboveground net primary production (ANPP) increased from early to mid CRP fields, where it reached its peak in 2005 and 2007 (127 g m^{-2} and 176 g m^{-2}, respectively; Fig. 4), and then decreased in late CRP fields. ANPP was not significantly different between late CRP fields seeded with native and introduced perennial grasses, except in 2007 when late CRP fields seeded with *Bromus inermis* had lower ANPP then late CRP fields seeded with native perennial grasses. Mid and late CRP fields had twice as much ANPP as undisturbed shortgrass steppe in 2005. Annual precipitation alone accounted for nearly half of the variance in ANPP in all CRP fields and undisturbed shortgrass steppe ($r^2 = 0.48$, $P < 0.0001$). Annual precipitation was a better predictor of ANPP in CRP fields seeded with native perennial grasses ($r^2 = 0.69$, $P < 0.0001$) than introduced perennial grasses ($r^2 = 0.28$, $P = 0.03$), whereas early growing season precipitation was a better predictor of ANPP in CRP fields seeded with introduced perennial grasses ($r^2 = 0.71$, $P < 0.0001$) than native perennial grasses ($r^2 = 0.09$, $P = 0.2$)

Litter biomass followed patterns of ANPP (Fig. 5), increasing between early and mid CRP fields and lower amounts in late CRP fields seeded with *Bromus inermis* compared to other late CRP fields. However, litter biomass positively correlated to ANPP from the previous year in late CRP fields ($r = 0.74$, $P = 0.0004$), where perennial grasses composed a majority of the biomass. There was no lag in early and mid fields where forbs and annuals dominated the plant community. Undisturbed shortgrass steppe had lower litter biomass than all CRP fields.

Belowground biomass in the top 5 cm of soil was 75 g m^{-2} 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. 6). Most of this increase was under perennial grasses, where biomass was 3.9 times higher in mid CRP fields and 4.6 times higher in late CRP fields relative to between perennial grasses (data not shown). Belowground 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 as much belowground biomass in the top 5 cm as CRP fields. There were no significant differences among CRP fields and between CRP fields and the shortgrass steppe in belowground biomass at depths below 5 cm. However, late fields seeded with introduced grasses had a more even depth distribution of roots than those seeded with native grasses and undisturbed shortgrass steppe. Belowground biomass at 5-10 cm was not significantly different than 0-5 cm in late CRP fields seeded with introduced perennial grasses. Furthermore, 60% of total belowground biomass was below 5 cm in these fields compared to 50% in late fields seeded with native grasses and 30% in undisturbed shortgrass steppe.

Belowground net primary production (BNPP) increased along the chronosequence in 2005, both when coarse roots were considered alone (2.4 g m^{-2} yr^{-1}) or together with fine roots and debris (3.4 g m^{-2} yr^{-1}; Fig. 7). In 2006, there was no significant change in BNPP along the chronosequence with either estimate, and in

2007 there was a decrease in BNPP when all fractions were considered. When background debris was accounted for in the 2007 BNPP estimates, there was no significant change in fine roots along the chronosequence, and an increase in coarse roots between mid and late CRP fields. In 2005 and 2007, there was significantly lower coarse root production in late CRP fields seeded with *Agropyron intermedium* compared to other late CRP fields. Undisturbed shortgrass steppe had high BNPP (208-235 g m^{-2}) relative to all CRP fields when estimates included all belowground material, except early CRP fields in 2007. Once background debris was accounted for in 2007 estimates, fine and coarse root production was collectively higher in undisturbed shortgrass steppe than CRP fields (not significant). Coarse root production was significantly higher in undisturbed shortgrass steppe compared to early and mid CRP fields in 2005, but there were no significant differences between undisturbed shortgrass steppe and all CRP fields in 2006 and 2007.

BNPP was significantly (1.3-2.8 times) higher under than between perennial grasses for all mid and late CRP fields seeded with native perennial grasses and undisturbed shortgrass steppe in all years (data not shown). These differences were only apparent in 2005 for late CRP fields seeded with introduced perennial grasses. The only significant interannual change in BNPP was an increase in early CRP fields. Annual precipitation was a poor predictor of BNPP in all CRP fields and undisturbed shortgrass steppe (data not shown), but explained some variability in coarse root production ($r^2 = 0.14$, $P = 0.006$).

Discussion

Time since CRP enrollment and seed mix explained differences in plant basal cover, density, and height. An increase in basal cover as time since CRP enrollment increased can be explained by the replacement of annual species with perennial grasses in CRP fields. This recovery of plant basal cover is important for soil organic matter input (Hook et al. 1991, Burke et al. 1995), forage production (O'Connor et al. 2001), and hydrologic and erosional processes (Gutierrez and Hernandez 1996). An increase of 0.89% basal cover per year is low compared with conversion from cultivated field to grassland in more mesic regions (Baer et al. 2002), but typical of the slow recovery of vegetation recovering from disturbance in the shortgrass steppe (Munson and Lauenroth, in press). Plant basal cover in late CRP fields seeded with native perennial grasses was half the basal cover of undisturbed shortgrass steppe, which suggests that full recovery of plant basal cover is not possible in twenty years under current CRP management practices. Plant basal cover was even lower in late CRP fields seeded with introduced rhizomatous perennial grasses, which can affect pools of carbon and nitrogen in soils (Derner and Briske 2001). Since basal cover was slow to change in CRP fields, it was not surprising that it was unresponsive to interannual changes in precipitation. Lane and others (1998) found that basal cover was not related to annual precipitation across a gradient from shortgrass steppe to tallgrass prairie. Plant basal cover is more likely to be limited by long-term mean annual precipitation at a site (Milchunas et al. 1989). Late CRP fields could have relatively low basal cover because there is a tradeoff with their other structural characteristics in a system limited by water availability (Chapin et al. 1993).

One indication of a structural characteristic tradeoff is that plant basal cover was inversely related to average plant height in late CRP fields and undisturbed shortgrass steppe during all years of the study ($r = 0.69$, $P < 0.0001$). This demonstrates that tall-growing plant communities did not have sufficient resources to also produce high basal cover. An increase in average plant height along the chronosequence is consistent with other recovering grasslands (Kahmen and Poschlod 2004) and can be attributed to the influence of perennial grasses. Although many annuals grew above 30 cm, most were relatively short in comparison to perennial grass height. Dominance of tall-growing perennial grasses in the two introduced seed mixes was a strong factor in explaining average plant height. Average plant height was low in undisturbed shortgrass steppe largely due to the dominance by short-growing perennial grasses. Low annual precipitation in 2006 likely caused a decrease in average plant height for all CRP fields and resulted in no height differences between late CRP fields seeded with introduced perennial grasses and native perennial grasses. Two consecutive dry early growing seasons reduced average plant height in late CRP fields seeded with introduced perennial grasses by half.

High plant density in early CRP fields can be attributed to the presence of annual species, which have high seed production, rapid dispersal, and high abundance in shortgrass steppe seedbanks (Coffin and Lauenroth 1989). As time since CRP enrollment increased, perennial grasses limited the abundance of annual species, which caused a decline in overall plant density. Intense competition by perennial grass roots for limited soil water (Aguilera and Lauenroth 1993) most likely drove this decline in the abundance of annual species. This effect of water limitation on annual species abundance was supported because differences in plant density among CRP fields only occurred in years when annual precipitation was above the mean. Wet years provided annuals with enough soil moisture to overcome the effects of competition with perennial vegetation. Low perennial grass density in late fields seeded with *Agropyron intermedium* may indicate another structural tradeoff when tall-growing perennial grasses grow in a water limited environment.

Although late CRP fields had low plant density, the average plant contributed 2-3 times as much to aboveground net primary production (ANPP) as early CRP fields, where plant density was high. This resulted in an increase in ANPP between early and late CRP fields in 2005 and no significant differences in 2006 and 2007. The peak in aboveground net primary production (ANPP) in mid CRP fields can be attributed to *Bromus tectorum*, which contributed 40% of ANPP to field level estimates in every year of the study. This exotic annual grass requires disturbance to establish in the shortgrass steppe (Bradford and Lauenroth 2006). Low initial seed availability or germination likely limited its contribution to ANPP in early CRP fields and competitive displacement by perennial grasses in late CRP fields.

Vegetation structure can constrain aboveground net primary production (Lauenroth and Sala 1992). An increase in perennial grass basal cover and density across the CRP chronosequence caused an increase in the relative contribution to ANPP of this functional type. As perennial grasses became the dominant life form in late CRP fields, differences in basal cover and height between CRP fields seeded with native and introduced grasses in 2005 did not lead to significant differences between these field types in ANPP. However, there were differences in the production of individual perennial grass units. When all late CRP fields were considered together, the amount of ANPP contributed per individual grass unit decreased as density increased according to a thinning law (Enquist et al. 1998) in 2005. In other words, an individual perennial grass unit was more productive when it occurred at low density. For example, *Agropyron intermedium* occurred at 1/3 the density of native perennial grasses in 2005, yet it produced up to 4 times as much per individual plant. This density-dependent effect was not apparent in 2006 and 2007 when early growing season precipitation reduced ANPP in fields seeded with *Agropyron intermedium* and *Bromus inermis*.

Annual precipitation has been shown to be related to ANPP in native shortgrass steppe (Lauenroth and Sala 1992) and cultivated fields (Lauenroth 2000). My results suggest that this relationship is supported in a transition between these two land cover types. CRP fields had more variability in ANPP because they had the potential to support twice as much ANPP as undisturbed shortgrass steppe in years 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 structure (Huxman et al. 2004). Mid CRP fields had the strongest response of ANPP to precipitation due to the presence of the annual grass, *Bromus tectorum*, which is sensitive to changes in water availability (Bradford and Lauenroth 2006). It was surprising that the ANPP of early CRP fields dominated by annual species did not respond more strongly to interannual variability in precipitation than late CRP fields dominated by perennial grasses, given that they respond more strongly to water additions in the shortgrass steppe (Lauenroth et al. 1978). Although annual precipitation influenced ANPP of CRP fields seeded with native C4 perennial grasses, early growing season precipitation was a better predictor of ANPP in fields with seeded with introduced C3 perennial grasses. This relationship is similar to the northern mixed-grass prairie (Derner and Hart 2007, Derner et al. 2008) where there are more C3, early-growing perennial grasses represented in the plant community.

High ANPP in CRP fields contributed to high aboveground litter compared to undisturbed shortgrass steppe. It is possible that tall vegetation structure in CRP fields may reduce wind speed at the soil surface, thereby reducing litter loss from the field (Burke et al. 1999). Large quantities of aboveground litter may have implications for decomposition and nutrient availability in CRP fields (Vinton and Burke 1995, Paschke et al. 2000). High ANPP and litter might also have caused a significant reduction in the amount of photosynthetically active radiation reaching the soil in late CRP fields relative to undisturbed shortgrass steppe (unpublished data). This reduction may inhibit seed germination and feedback into plant community composition (Milchunas and Lauenroth 1995). Patterns of litter biomass in CRP fields were closely related to ANPP. However, the lag between ANPP and litter biomass varied with CRP field type. In late CRP fields, dry years resulted in less ANPP and less litter the following year; whereas in early and mid CRP fields, dry years resulted in less ANPP and litter biomass in the same year. The lag time of litter biomass in late CRP fields can be attributed to the slower turnover of perennial compared to annual plant parts (Vinton and Burke 1995).

In contrast to high ANPP and aboveground litter biomass, belowground biomass in CRP fields was significantly lower than undisturbed shortgrass steppe. This was not a result of lower belowground biomass under native perennial grasses in CRP fields, but rather more plant interspace and less root biomass in the plant interspace in CRP fields relative to undisturbed shortgrass steppe. This suggests that perennial grasses in CRP fields have not had the time to develop the extensive root structure of undisturbed shortgrass steppe (Sims and Singh 1978b) and root growth may be limited by low vegetation basal cover. The implications for relatively low belowground biomass may be susceptibility to grazing or drought over the long-term, conditions to which undisturbed shorgrass steppe is well adapted (Milchunas et al. 1988). Early CRP fields lacked perennial grasses when biomass samples were taken, and therefore had low belowground biomass relative to mid and late CRP fields. Although there were no significant differences in belowground biomass between late CRP fields seeded with native and introduced perennial grasses at the field scale, there was significantly lower biomass under introduced perennial grasses at the plant scale. This is likely because these grasses have rhizomes, which spread root growth horizontally away from the center of the aboveground plant. Low belowground biomass under introduced perennial grass shoots may limit carbon and nitrogen accumulation in soils (Derner and Briske 2001) and small-scale nutrient heterogeneity (Hook et al. 1991).

Belowground net primary production (BNPP) was likely overestimated when all fractions were included together and underestimated with only coarse roots. The high end of my estimate for BNPP in undisturbed shortgrass steppe (208-235 g m^{-2}) is comparable to the carbon tracer estimate found by Milchunas and Lauenroth (1992) (202-262 g m^{-2}). However, when background debris was accounted for in 2007, my estimate in undisturbed shortgrass steppe was 107 g m^{-2}. This estimate may have been low because I only sampled root production between May and September, and root growth may have occurred before or after this time. Furthermore, I sampled the center of the ingrowth core, missing the outer perimeter where root growth into the core may have been higher.

As with belowground biomass, BNPP increased along the chronosequence in 2005. This was due to the contribution of BNPP from perennial grasses in late CRP fields, which allocate more resources belowground than annual species (Zangerl and Bazzaz 1983, Jackson and Roy 1986, Ploschuk et al. 2005). The influence of perennial grasses on BNPP was most evident in early CRP fields, where their establishment contributed to an increase of BNPP in early CRP fields during the three-year study. Annual species likely contributed little to this increase in BNPP because they declined in abundance over the same time period. There were no differences in BNPP among CRP fields in 2006, when annual precipitation was below the mean. This was also the pattern in ANPP, collectively providing strong evidence that low water availability masks the affects of vegetation structure on total net primary production (Huxman et al. 2004). Only in wet years can vegetation structure limit the capacity of plants to increase total net primary production (Yahdjian and Sala 2006).

High ANPP to BNPP ratios in CRP fields relative to undisturbed shortgrass steppe is typical of fields after the cessation of cropping (Paschke et al. 2000), and indicates the potential for high transpiration water losses relative to a limited capacity to take up water. Large reductions in the ANPP:BNPP ratio in all CRP fields in the driest year of this study suggests that high aboveground tissue cannot be supported in the long-term (Burke et al. 1998). The best example of this occurred in CRP fields seeded with *Agropyron intermedium*. These fields had lower coarse root production than other late CRP fields in the three years of the study and consequently had the largest reduction in ANPP in dry years. Late CRP fields seeded with *Agropyron intermedium* and *Bromus intermis* had lower fine-scale spatial heterogeneity in BNPP than native perennial grasses, which supports the patterns in belowground biomass.

Interannual variability in precipitation did not explain patterns in BNPP (all fractions), which had low interannual variance during the study, except in early CRP fields. BNPP may be slower to change in response to precipitation than ANPP (Gill and Jackson 2000, Milchunas and Lauenroth 2001). However, my estimates of BNPP included some non-root material. When coarse roots were isolated from the samples, production increased with annual precipitation, which is consistent with interannual changes at the shortgrass steppe study site (Milchunas and Lauenroth 2001). A better assessment of what constitutes an estimate of belowground net primary production is necessary, especially in belowground dominated grassland ecosystems.

Literature Cited

Aguilera, M.O., and W.K. Lauenroth. 1993. Seedling establishment in adult neighbourhoods: intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. Journal of Ecology 81: 253-261.

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12: 1688-1701.

Bazzaz, F.A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259-275 *in* H. A. Mooney and M. Godron, eds. Disturbance and ecosystems: components of response. Springer-Verlag, Berlin.

Bradford, J.B., and W.K. Lauenroth. 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance, and seed availability. Journal of Vegetation Science 17: 693-704.

Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Science Society of America Journal 53: 800-805.

Burke, I.C., W.K. Lauenroth, and D.P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program. Ecological Applications 5: 793-801.

Burke, I.C., W.K. Lauenroth, M.A. Vinton, P.B. Hook, R.H. Kelly, H.E. Epstein, M.R. Aguiar, M.D. Robles, M.O. Aguilera, K.L. Murphy, and R.A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42: 121-143.

Burke, I.C., W.K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe : the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2: 422-438.

Chapin, F.S. III, K. Autumn, and F. Pugnaire. 1993. Evolution of suites of traits in response to environmental stress. American Naturalist 142: S78-S92.

Chapin, F.S. III, E.S. Zavaleta, V.T. Eviner, V.T., R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack, and S. Diaz. 2000. Consequences of changing biotic diversity. Nature 405: 234–242.

Christian, J.M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. Ecology 80: 2397-2407.

Coffin D. P., and W.K. Lauenroth. 1988. The effects of disturbance size and frequency on a shortgrass community. Ecology. 69: 1609–1617.

Coffin, D. P., and W.K. Lauenroth. 1989. The spatial and temporal variability in the seed bank of a semiarid grassland. American Journal of Botany 76: 53-58.

Coffin, D.P., W.K. Lauenroth, and I.C. Burke. 1996. Recovery of Vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications 6: 538-555.

Derner, J.D., and D.D. Briske. 2001. Below-ground carbon and nitrogen accumulation in perennial grasses: A comparison of caespitose and rhizomatous growth forms. Plant and Soil 237: 117-127.

Derner, J.D., and R.H. Hart. 2007. Grazing-induced modifications to peak standing crop in northern mixed-grass prairie. Rangeland Ecology and Management 60: 270-276.

Derner, J.D., B.W. Hess, R.A. Olson, and G.E. Schuman. 2008. Functional group and species responses to precipitation in three semi-arid rangeland ecosystems. Arid Land Research and Management 22: 81-92.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4: 412-417.

Enquist, B.J., J.H. Brown, and G.B. West. 1998. Allometric scaling of plant energetics and population density. Nature 395:163-166.

Fair, J.L., W.K. Lauenroth, and D.P. Coffin. 1999. Demography of *Bouteloua \ gracilis* in mixed prairie: analysis of genets and individuals. Journal of Ecology 87: 233-243.

Gill, R.A., and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytologist 147: 13-31.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169-1194.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, U.K.

Gutierrez, J., and I.I. Hernandez. 1996. Runoff and interrill erosion as affected by grass cover in a semi-arid rangeland of northern Mexico. Journal of Arid Environments 34: 287–295.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138: 247-256.

Hook, P.B., I.C. Burke, and W.K. Lauuenroth. 1994. Spatial patterns of plant cover and roots in a semiarid grassland: abundance of canopy openings, root gaps, and resources gaps. Journal of Ecology 82: 485-494.

Huxman, T.E., M.D. Smith, P.A. Fay, A.K. Knapp, M.R. Shaw, M.E. Loik, S.D. Smith, D.T. Tissue, J.C. Zak, J.F. Weltzin, W.T. Pockman, O.E. Sala, B.M. Haddad, J. Harte, G.W. Koch, S. Schwinning, E.E. Small, and D.G. Williams. 2004. Convergence across biomes to a common rain-use efficiency. Nature 429: 651-654.

Jackson, L. E., and J. Roy. 1986 Growth patterns of mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California. Oecologia Plantarum 7: 191–212.

Jordan, C.F., and G. Escalante. 1980. Root productivity in an Amazonian rain forest. Ecology 61: 14-18.

Kahmen, S., and P. Poschlod. 2004. Plant functional trait response to grassland succession over 25 years. Journal of Vegetation Science 15: 21-32.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157–164.

Lane, D. R., D. P. Coffin, and W. K. Lauenroth. 1998. Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States. Journal of Vegetation Science 9: 239–250.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36: 211-222.

Lauenroth, W.K., and D.P. Coffin. 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. Pages 131-150 *in* M.K. Wali, ed. Ecosystem rehabilitation: preamble to sustainable development. Volume 2: Ecosystem analysis and synthesis. SPB Academic Publishing, The Netherlands.

Lauenroth, W. K., and Milchunas, D. G. 1992. Short-grass steppe. Pages 183-226 *in* Coupland, R. T., ed. Ecosystems of the World 8A, Natural Grasslands, Introduction and Western Hemisphere. Elsevier, New York.

Lauenroth, W.K., and O.E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2: 397-403.

Lauenroth, W.K., I.C. Burke, and J.M. Paruelo. 2000. Patterns of production and precipitation use efficiency in winter wheat and native grasslands in the central Great Plains of the United States. Ecosystems 3: 344-351.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16: 545-556.

Lieth, H., and R.H. Whittaker, eds. 1975. Primary productivity of the biosphere. Ecological Studies, v. 14. Springer-Verlag, New York.

MacMahon, J.A. 1980. Ecosystems over time: succession and other types of change. Pages 27-58 *in* Waring, R.H., ed. Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis.

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., 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., and W.K. Lauenroth. 1992. Carbon dynamics and estimates of primary production by harvest, ^{14}C dilution and ^{14}C turnover. Ecology 73: 593-607.

Milchunas, D.G., and W.K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Ecological Applications 5: 452-458.

Milchunas, D.G., and W.K. Lauenroth. 2001. Belowground primary production by carbon isotope decay and long-term root biomass dynamics. Ecosystems 4: 139-150.

Munson, S.M., and W.K. Lauenroth. In press. Plant population and community responses to removal of the dominant species in the shortgrass steppe. Journal of Vegetation Science.

Natural Resources Conservation Service. 1991. Technical Guide, Section IV, Standards and Specifications, Range Seeding, Colorado. USDA, Colorado.

O'Connor, T. G., L. M. Haines, and H. A. Snyman. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. Journal of Ecology 89: 850–860.

Paschke, M., T. McLendon, and E. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3: 144-158.

Pickett, S.T.A., and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

Ploschuk, E.L., G.A. Slafer, and D.A. Ravetta. 2005. Reproductive allocation of biomass and nitrogen in annual and perennial *Lesquerella* crops. Annals of Botany 96: 127-135.

Redente, E.F., M.E. Biondini, and J.C. Moore. 1989. Observations on biomass dynamics of a crested wheatgrass and native shortgrass ecosystem in southern Wyoming. Journal of Range Management 42: 113-118.

Seabloom, E.W., W.S. Harpole, O.J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences 100: 13384–13389.

Sims, P. L., and J. S. Singh. 1978a. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer compartments. Journal of Ecology 66: 547-572.

Sims, P. L., and J. S. Singh. 1978b. The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. Journal of Ecology 66: 573-597.

Skold, M.D. 1989. Cropland retirement policies and their effects on land use in the Great Plains. Journal of Production Agriculture 2: 197-201.

Smith, T.M., and M.A. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83: 49-69.

Smucker, A.J.M., McBurney, S.L., and Srivastava, A.K. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agronomy Journal 74: 500-503.

Stevens, P.R., and T.W. Walker. 1970. The chronosequence concept and soil formation. Quarterly Review of Biology 45: 333-350.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton.

USDA Farm Service Agency. 2008. U.S. Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 31 July 2008). 4 November 2008 from: http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM

USDA National Agricultural Statistics Survey. 2008. Quick Stats: Agricultural Statistics Data Base. 4 November 2008 from: http://www.nass.usda.gov/QuickStats

Vinton M.A. 1994. The influence of individual plants on soil nutrient dynamics in the central grassland region of the United States. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado.

Vinton, M.A., and I.C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76: 1116-1133.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes; towards an integration of population biology and ecosystem studies. Oikos 57:7-13.

Wedin, D. A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science 274: 1720-1723

Woodward, F.I., and A.D. Diament. 1991. Functional approaches to predicting the ecological effects of global change. Functional Ecology 5: 202-212.

Yahdjian, L., and O.E. Sala. 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. Ecology 87: 952-962.

Zangerl, A.R., and F.A. Bazzaz. 1983. Plasticity and genotypic variation in photosynthetic behavior of an early and a late successional species of *Polygonum*. Oecologia 57: 270-273.

Year	2005	2006	2007	38-year Average
Annual Precipitation (Jan-Dec)	370	301	409	332
Early Growing Season Precipitation (Apr-Jun)	202	54	82	143
Late Growing Season Precipitation (Jul-Sep)	53	144	224	124

Table 1. Annual and seasonal precipitation (mm) from 2005-2007.

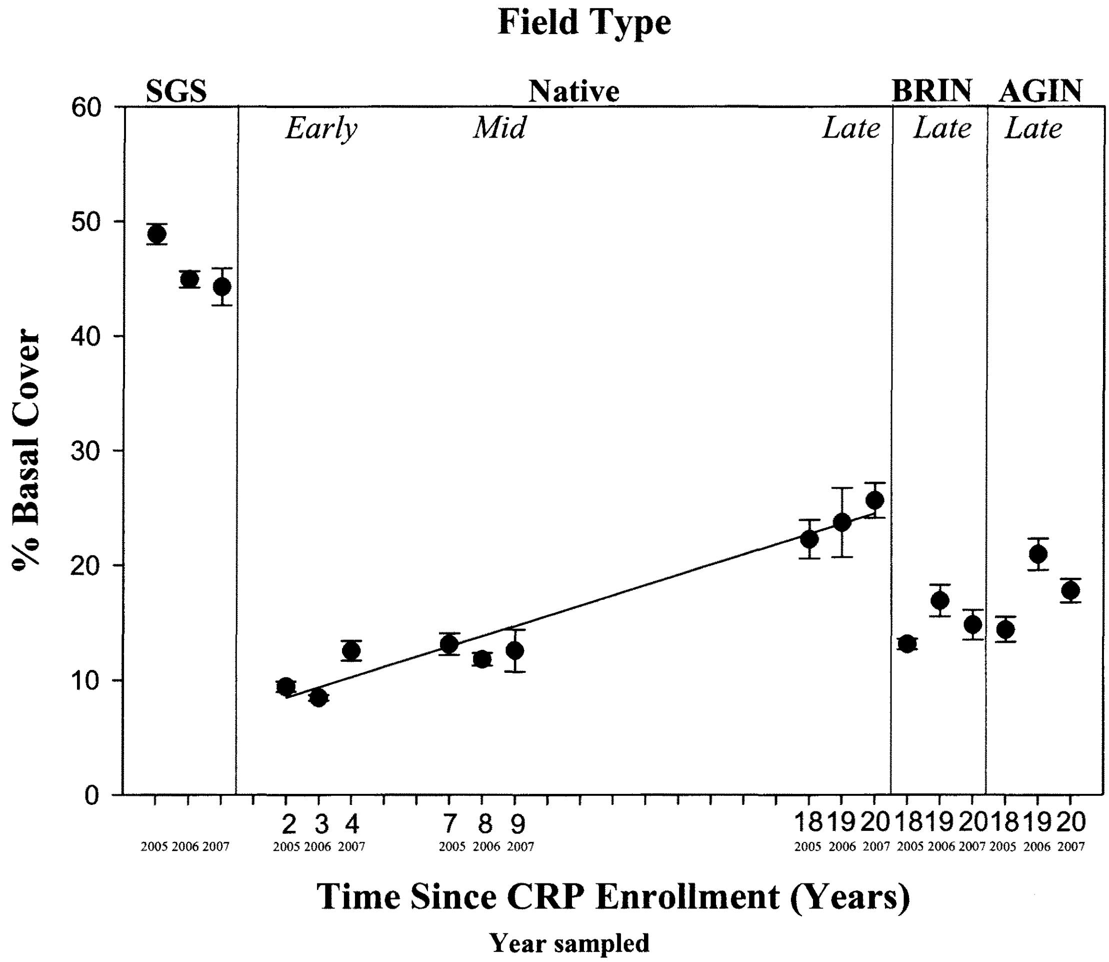


Figure 1. Average plant basal cover (± SE) in undisturbed shortgrass steppe (SGS), early, mid and late CRP fields seeded with a native seed mix, and late CRP fields seeded with Bromus inermis (BRIN) and Agropyron intermedium (AGIN) in 2005, 2006, and 2007. Chronosequence linear regression: $y = 0.89x + 6.6$, $r^2 = 0.85$.

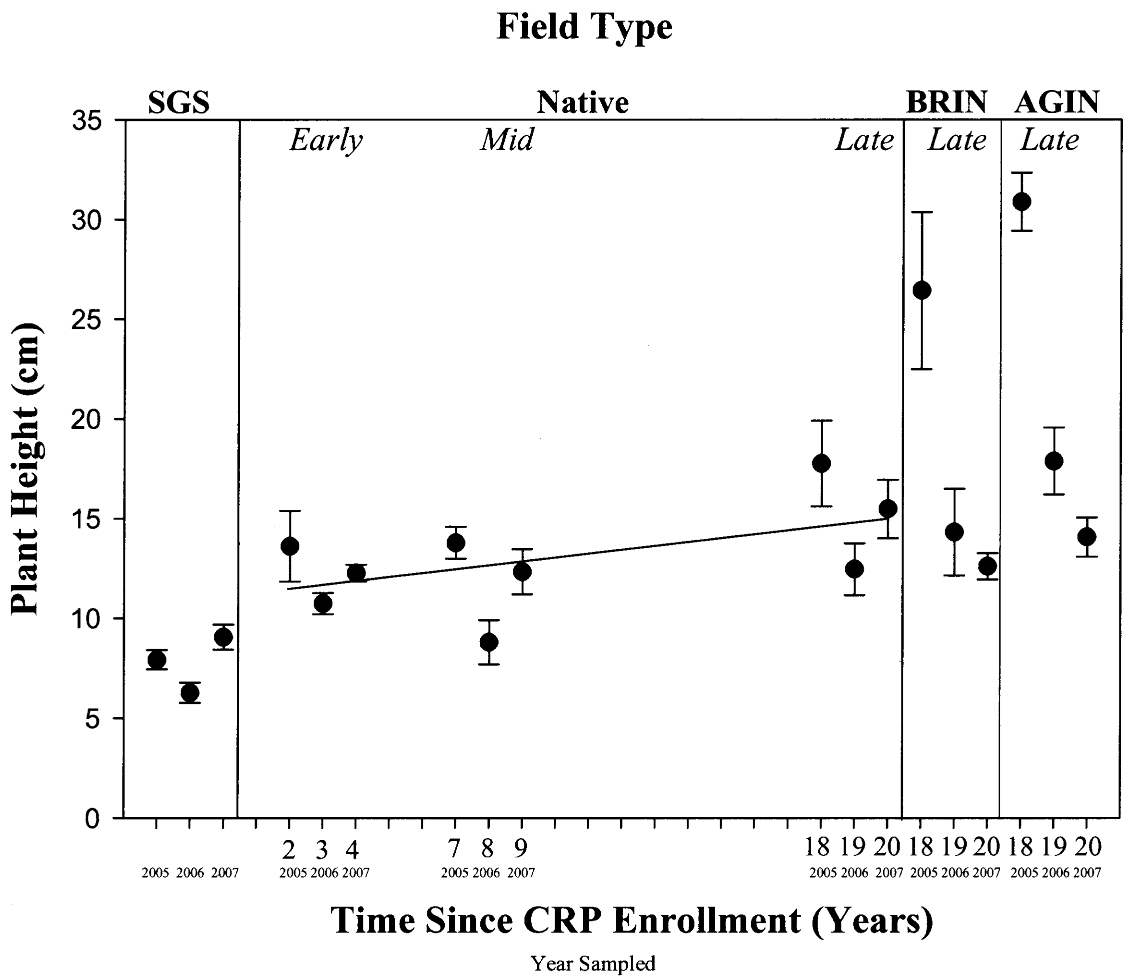


Figure 2. Average plant height (± SE) in undisturbed shortgrass steppe (SGS), early, mid and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006, and 2007. Chronosequence linear regression: $y = 0.20x + 11$, $r^2 = 0.19$.

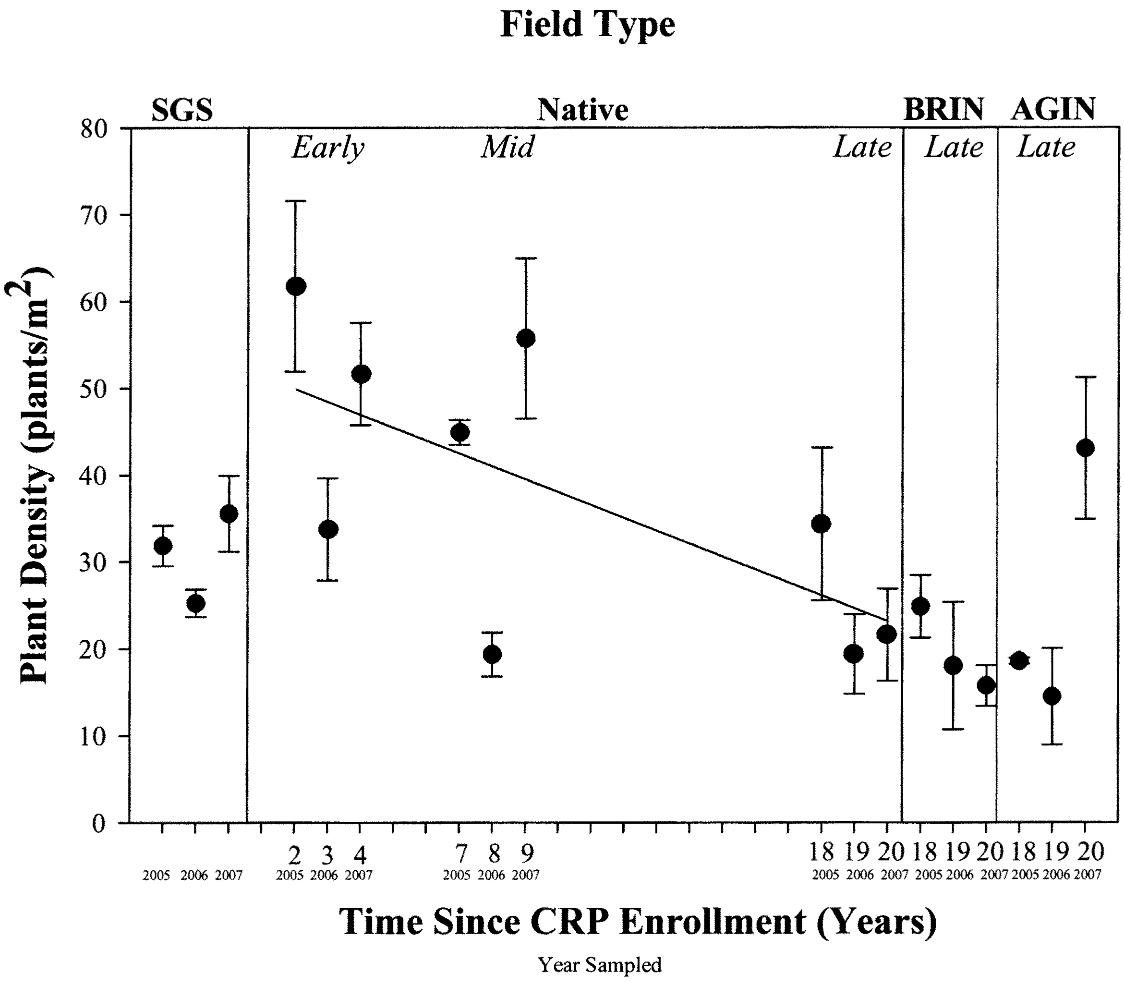


Figure 3. Average plant density (± SE) in undisturbed shortgrass steppe (SGS), early, mid and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006, and 2007. Chronosequence linear regression: $y = -1.5x + 53$, $r^2 = 0.31$.

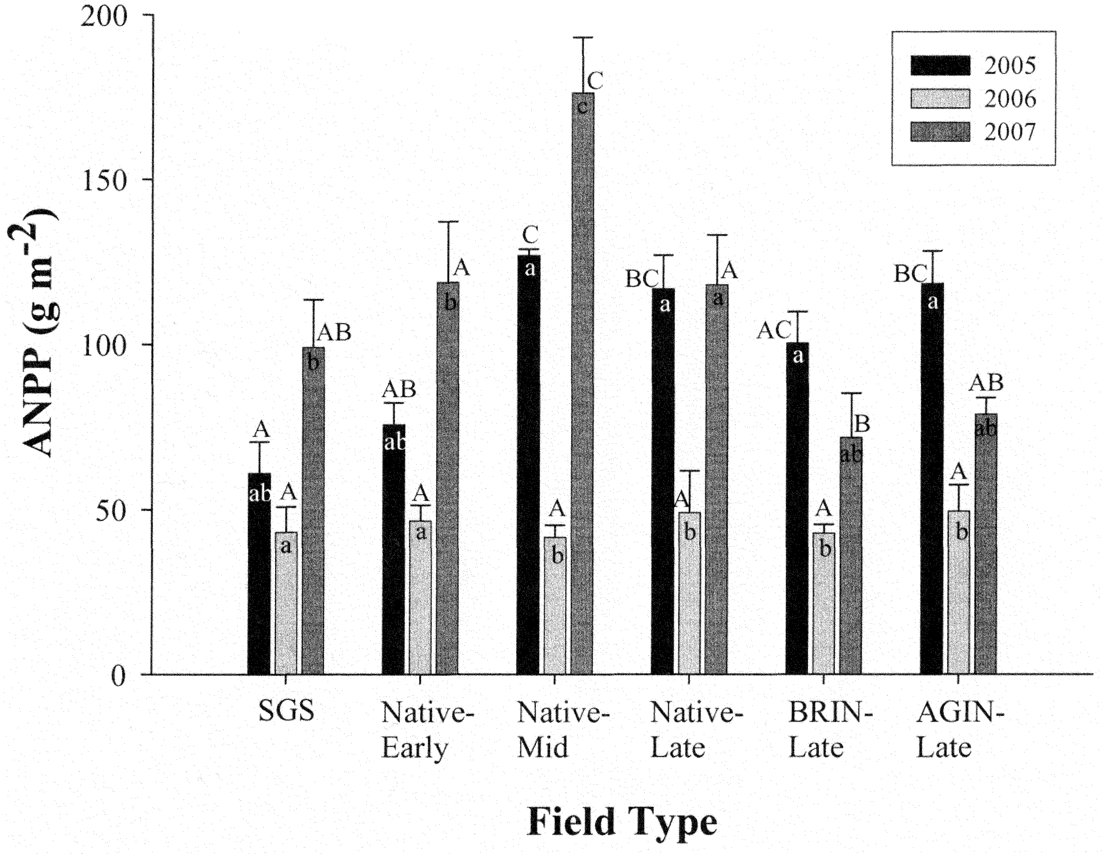


Figure 4. Aboveground net primary production (ANPP g m^{-2}; ± SE) in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006, and 2007. Different upper 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.

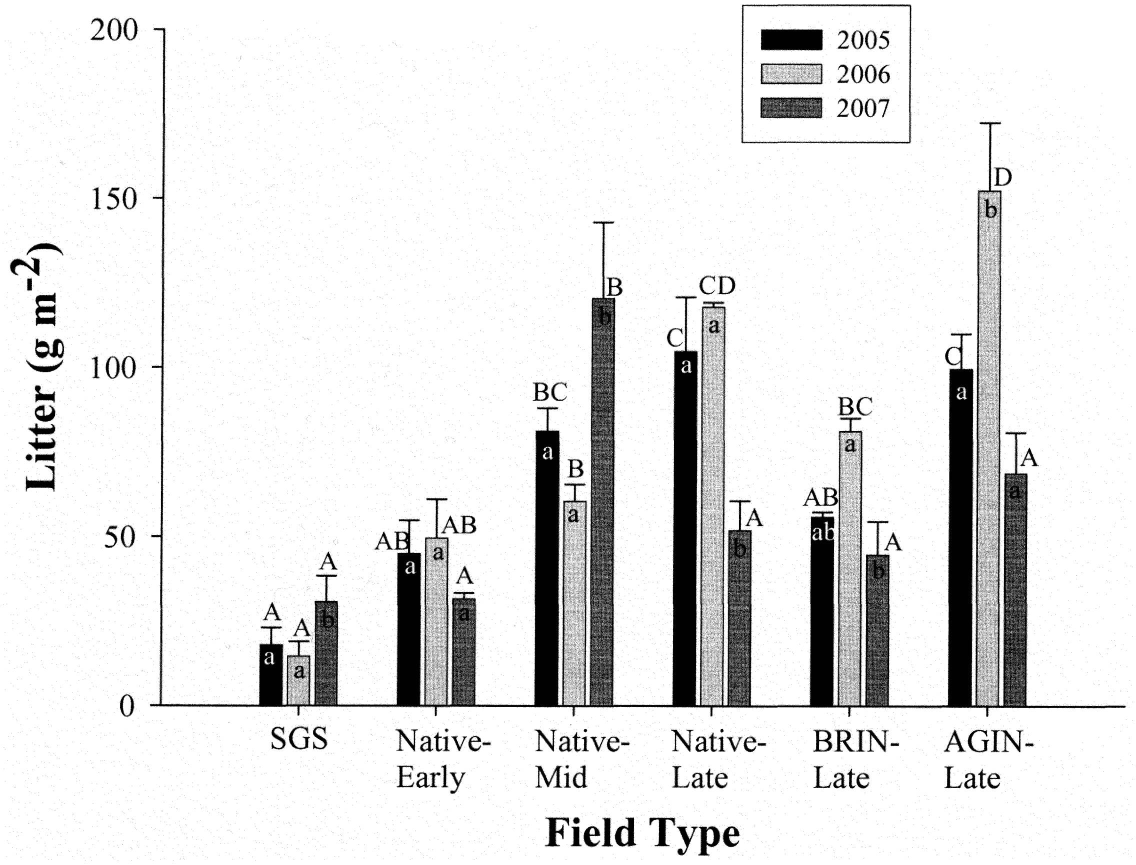


Figure 5. Litter (g m^{-2}; ± SE) in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005, 2006, and 2007. Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in litter among field types within the same sampling year, and different lower case letters designate significant differences (Tukey adjusted $P < 0.05$) in litter among years within the same field type.

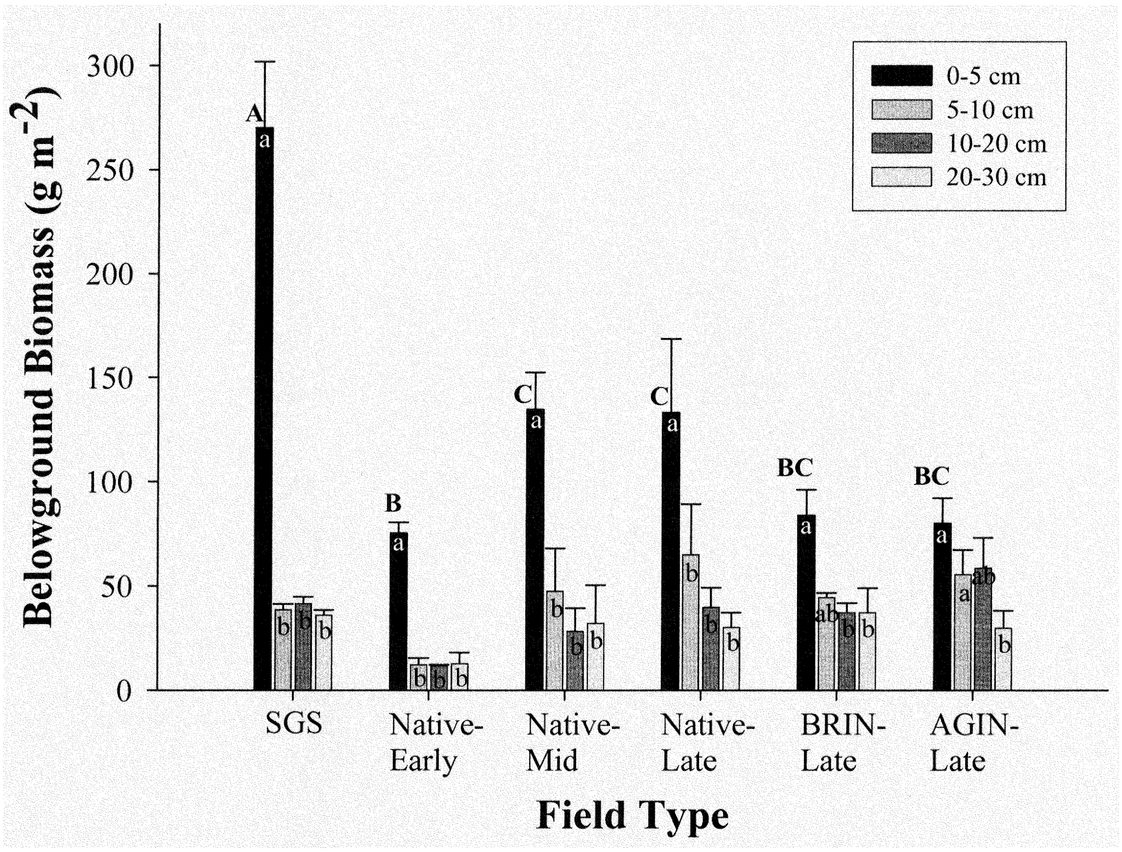
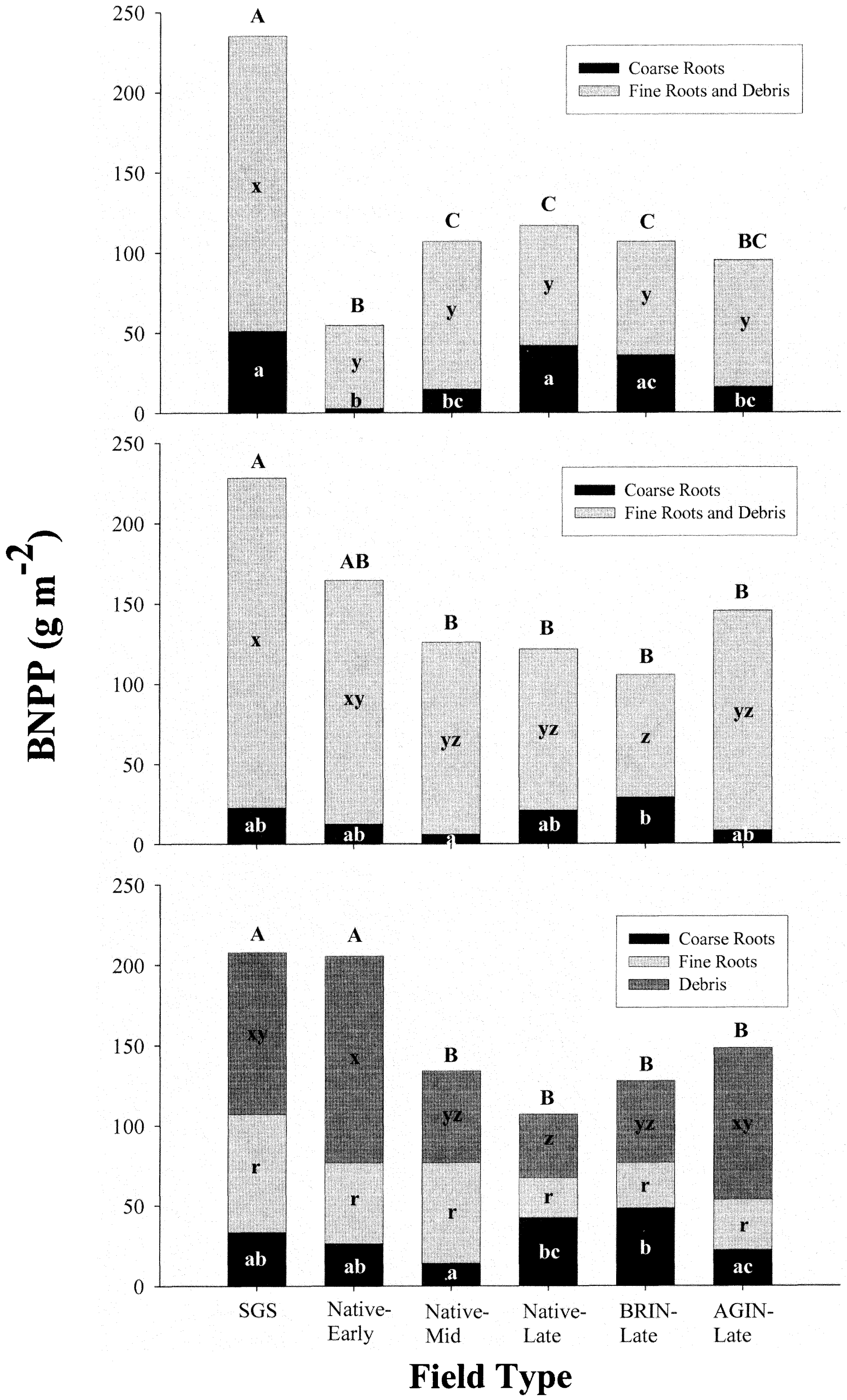


Figure 6. Belowground biomass (g m^{-2}; ± SE) at 0-5, 5-10, 10-20, and 20-30 cm depth in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005. Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in belowground biomass at 0-5 cm depth among field types. There were no significant differences in belowground biomass at all other depth increments among field types. Different lower case letters designate significant differences (Tukey adjusted $P < 0.05$) in belowground biomass among depth increments within the same field type.


BNPP (g m-2)
250
200
150
100
50
0
A
x
a
B
y
b
C
y
bc
C
y
a
C
y
ac
BC
y
bc
Coarse Roots
Fine Roots and Debris
A
x
ab
AB
xy
ab
B
yz
a
B
yz
ab
B
z
b
B
yz
ab
Coarse Roots
Fine Roots and Debris
A
xy
r
ab
A
x
r
ab
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yz
r
a
B
z
r
bc
B
yz
r
b
B
xy
r
ac
Coarse Roots
Fine Roots
Debris
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
Field Type

Figure 7. Belowground net primary production (BNPP g m^{-2}; ± SE) in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005 (top panel), 2006 (middle panel) and 2007 (bottom panel). BNPP is partitioned into coarse roots, fine roots, and debris. Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in total BNPP among field types. Different lower case letters designate significant differences (Tukey adjusted $P < 0.05$) in coarse roots, fine roots, and debris among field types. There were no significant differences in BNPP among years within the same field type except in early CRP fields.

Chapter 4: Soil Carbon and Nitrogen Changes on Conservation Reserve Program Lands in Northeastern Colorado

Introduction

Human-induced land use change can rapidly alter the carbon (C) cycle in ecosystems (Vitousek et al. 1997). Since soil organic carbon (SOC) is the largest terrestrial pool of organic C (Schimel 1995) and has a long residence time (Oades 1988), it is important to understand how the size and dynamics of this reservoir may be altered (Paul 1984). Of increasing concern is how the potential of ecosystems to remove and store anthropogenic sources of carbon from the atmosphere may be modified (Lal 2004, IPCC 2007). Since carbon uptake and storage is tightly linked to the nitrogen (N) cycle (Vitousek and Howarth 1991, Diaz et al. 1993), it is equally important to understand how N pools and fluxes may be affected by land use change. Much effort has been made to elucidate global controls regulating inputs and outputs of SOC using meta-analysis (Post et al. 1982, Post and Kwon 2000) and modeling (Parton et al. 1987) approaches, while less effort has been made to link SOC to exchanges with the vegetation and atmosphere using an empirical approach. Characterization of SOC in the context of its gains and losses can lead to a mechanistic understanding of its dynamics (Odum 1960) and improve our ability to predict how ecosystems respond to land use change.

Conversion of natural to cultivated ecosystems is a well-studied land use change that has historically transferred between 54-70 Gt (Gt = 10^{12} kg) of C from the soil to the atmosphere (Cole et al. 1997, Amundson 2001). This has resulted in reductions of SOC by up to 60% (Guo and Gifford 2002) through reduced plant inputs into SOC and increased outputs, including erosion and decomposition

(Anderson and Coleman 1985). Cessation of cropping and establishment of perennial vegetation can promote the recovery of SOC pools (Conant et al. 2001), but rates of accumulation depend on the productivity of the recovering vegetation, soil physical and biotic factors, and the potential for losses (Post and Kwon 2000). In the shortgrass steppe, a semiarid grassland of the Great Plains, high allocation of net primary production to roots, high turnover of plant biomass, and slow decomposition rates create potential for SOC storage (Burke et al. 2008). Recovery of the shortgrass steppe plant community following cropping disturbance is slow and variable (Coffin et al. 1996), and successional plant communities in formerly cultivated fields may differ in the quantity and quality of plant inputs to SOC. Outputs from SOC, including soil respiration may also vary in recovering fields due to changes in the plant and microbial community, soil resources and physical characteristics.

The conversion from cultivated fields to perennial vegetation has been assisted by seeding practices of the Conservation Reserve Program (CRP; Skold 1989). CRP is an extensive land use nationwide and currently includes nearly 1 million hectares of former shortgrass steppe in Colorado (USDA Farm Service Agency 2008). CRP contracts are for 10 years, but many fields have been reenrolled in the program and have been out of production for two decades. This has created an opportunity to determine SOC recovery at a longer time scale than most CRP studies (Robles and Burke 1997, Reeder et al. 1998, Baer et al. 2000), while accounting for seed mix and potential plant community composition, which is lacking in long-term studies (Burke et al. 1995, Breuer et al. 2006, Kucharik et al. 2006).

Time since CRP enrollment and seed mix are important factors for plant community composition (Chapter 2) and associated plant characteristics (Chapter 3). Early CRP fields (2-4 years after CRP enrollment) are composed of a species rich forb and annual grass community. Low basal cover and high annual turnover of these species may limit their effect on SOC recovery. Perennial grasses, which dominate the CRP plant community within 18 years, are more likely to increase SOC due to increased basal cover, high belowground net primary production, and long life-span. However differences in recovery rate, allocation, and tissue quality between native and introduced perennial grasses may influence the recovery of SOC (Christian and Wilson 1999, Ogle et al. 2004).

The objective of my study was to determine how effective CRP fields are in storing carbon and nitrogen. To evaluate this, I addressed the following questions:

1) How does time since CRP enrollment and seed mix influence SOC and soil nitrogen?
2) How does time since CRP enrollment and seed mix influence plant inputs and respiration outputs that control C storage?
3) What is the relationship between SOC and nitrogen availability in CRP fields?

Methods

Study sites

My study was conducted at undisturbed shortgrass steppe sites within the Central Plains Experimental Range (CPER, Shortgrass Steppe Long Term Ecological Research site) located 60 km northeast 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. Mean annual precipitation at the CPER is 332 mm ($\sigma = 99$ mm), 80% of which falls between April and September, and mean annual temperature is 9.6°C ($\sigma = 1.1$°C). Undisturbed shortgrass steppe is co-dominated by the C_4 perennial grasses *Bouteloua gracilis*[*] and *Buchloë dactyloides*, with other important functional types including C_3 graminoids, forbs, dwarf shrubs, and prickly pear cactus (Lauenroth 2008). My shortgrass steppe sites had been long-term moderately summer grazed, but I excluded them from grazing during the study.

I divided CRP sites into those seeded with native and introduced perennial grasses. The native seed mix contained *Agropyron smithii* (~ 30% weight of all seed), *Bouteloua 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 time since CRP enrollment, I established a chronosequence (Stevens and Walker 1970), which consisted of three field ages: early (2 years after CRP enrollment), mid (7 years), and late (18 years). I only included fields seeded with a native seed mix in the chronosequence to minimize differences in the potential vegetation. To address differences in seed mix, I controlled for field age and compared late CRP fields seeded with native perennial grasses to late CRP fields seeded with introduced perennial grasses..

All fields were in a non-irrigated wheat-fallow rotation prior to CRP enrollment. The year of CRP enrollment, fields were seeded with a sterile sorghum

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[*] plant names follow Great Plains Flora Association 1986

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 (~ 0.5 g m^{-2} seed) to a 1.3 cm depth and 20 cm spacing between rows. Soils at the sites were classified as Altvan and Ascalon fine sandy loams (mixed, mesic Aridic Argiustoll), with a minor component of Renohill Shingle Complex (smectitic, mesic Ustic Haplargid). These soils were deep and well drained (NRCS 2008). All sites had a similar topographic relief (< 3% slope). I replicated each of the six field types three times for a total of eighteen fields sampled (6 field types x 3 field replicates = 18 fields sampled).

Sampling methods

I estimated aboveground net primary production (ANPP) in each field in late August 2005. Aboveground biomass was clipped at the soil surface in 8 ¼ m^2 quadrats, which were evenly spaced 40 m apart. Dead biomass from previous growing seasons was sorted out of the samples, and the remaining sample was weighed after oven drying at 55°C for 48 hours. ANPP estimates of *Bromus tectorum*, an introduced winter annual grass species, were made at the end of its growing season in early June and incorporated into field estimates. I estimated belowground net primary production (BNPP) in each field by constructing a root ingrowth core (Jordan and Escalante 1980). To do this, I removed eight soil cores (5 cm in diameter and 30 cm in depth) adjacent to the ANPP plots in early May directly under the dominant perennial grass and eight cores from the nearest plant interspaces (10 cm away from nearest plant). This microsite sampling stratification encompassed spatial variation in root production (Hook et al. 1994). Sampling was not stratified in early CRP fields because there were no perennial grasses. I separated soils from a 0-5 cm depth from the cores and oven dried them 48 hours to use for soil analyses. The holes from the cores were filled with root free soil, which I collected from each field and dry sieved through wire screen (1mm aperture) to remove roots and organic debris. The ingrowth cores were left in the ground until the following October. At this time, I recored the ingrowth cores using a cylinder with slightly smaller dimensions than the first (4.5 cm in diameter and 25 cm in depth) to minimize sampling outside the ingrowth area. I separated roots from ingrowth cores using a hydropneumatic root elutriator (Smucker et al. 1982).

Both ANPP and BNPP were expressed in g C m^{-2} and g N m^{-2} by determining the amount of carbon and nitrogen in NPP estimates. This was done using aboveground plant tissue from a subset of 3 ANPP quadrats (N = 3) and a composite of root tissue from 8 ingrowth cores (N = 1) under perennial grasses in each field. I ground all samples in a Wiley mill and then analyzed them for carbon and nitrogen concentration in a LECO CHN-2000 Combustion Analyzer (Leco Corp., St. Joseph, MI, USA). Remaining ANPP and BNPP samples were ashed in an Isotemp Muffle Furnace (Model 550-126; Fisher Scientific, Pittsburgh, PA, USA) at 550°C to determine the amount of carbon and nitrogen on an ash-free basis.

I calculated soil bulk density from the oven-dried soil weights of samples collected at a 0-5 cm depth. Soil C and N was estimated at the same depth because surface soils have the highest concentration of roots and recent soil organic matter inputs (Burke et al. 2008). I sieved soil samples to remove plant material > 2 mm in diameter and used 30 g subsamples to determine soil texture by the hydrometer method (Day 1965). Soils were then composited in random pairs from the same field and microsite (either between or under perennial grass; N = 4) and analyzed for total C and total N, as well as C and N in the particulate organic matter (POM) fractions (Cambardella and Elliott 1992). To determine POM fractions, I dispersed 30 g subsamples of soil on a shaker using sodium hexametaphosphate and passed them through two sieves with apertures of 500- and 53 µm. Coarse POM was retained on the 500 µm sieve and fine POM was retained on the 53 µm sieve. Residue and sand in these fractions were oven dried at 55°C and ground on a ball mill. Although carbonates can contribute to soil carbon, there is low inorganic carbon in the surface of soils in the shortgrass steppe region (Reeder et al. 2004) and my soil samples did not react visibly to drops of HCl. Soil carbon was therefore considered organic carbon (SOC). I analyzed total, coarse and fine POM fractions for C and N on a LECO CHN-1000 analyzer (LECO Corporation, St. Joseph, MI, USA).

I used ion exchange resin bags to estimate in situ inorganic soil nitrogen (Binkley and Matson 1983) adjacent to the NPP plots. Estimates were made from 2005-2007 to account for environmental variability. I installed the bags 5 cm below the soil surface at each microsite (between and under perennial grasses) in May and collected the bags in September. Inorganic nitrogen (nitrate and ammonium) was extracted from the bags using a KCl solution and their concentrations were colorimetrically determined with an Alpkem Flow Solution Autoanalyzer (Alpkem Corporation, Clackamas, OR, USA). There were some interannual differences of when in May the resin bags were installed and when in September they were collected. To account for this variability, I standardized measurements by converting to a daily rate of inorganic nitrogen adsorption (μg N bag^{-1} day^{-1}).

To characterize carbon losses, I determined the soil respiration rates of early and late CRP fields in the chronosequence and undisturbed shortgrass steppe using a LI-6400 soil CO_2 flux chamber (chamber volume: 991 cm^3; LI-COR, Inc., Lincoln, NE, USA). I replicated each field type three times. I used the average CO_2 flux rate during 5 sampling periods between June 11, 2007 and July 25, 2007 between the times of 08:00 and 13:00. Volumetric water content during the sampling periods was below 3% and soil temperature in the top 5 cm of the soil was 23 - 30°C. Since water limits respiration in the shortgrass steppe (Munson et al., in review), these dry conditions likely produced minimum (baseline) respiration rates. To determine soil respiration rates when soil water was not limiting, I took measurements during the last sampling period before and after a 10 mm simulated precipitation event, which increased soil water content by 300% or more relative to pre-event conditions (Munson, in review). Precipitation of this event size occurs at the shortgrass steppe during a normal growing season (Sala and Lauenroth 1982), and soil respiration that results from an event this size was determined not to be limited by soil moisture (Munson et al., in review). I used the maximum respiration rate recorded during a 24 hour period after the event. All respiration measurements were taken in the plant interspace (to minimize the influence of aboveground plant respiration and soil resource heterogeneity) from 4 chamber locations within a 1.5 m^2 plot.

To determine if nitrogen constrains NPP and soil respiration in early and late CRP fields in the chronosequence and undisturbed shortgrass steppe, I applied 8 g N

m^{-2} in the form of ammonium nitrate (NH_4NO_3) granules to a 1.5 m^2 plot located 3 m from the water addition plot in May 2007. I used adjacent unfertilized 1.5 m^2 plots as a control. I added this quantity of N to the plot based on previous findings indicating an increase in plant and microbial activity (Lowe 2002). I replicated each field type three times. Two weeks after fertilization, I took soil respiration readings using the methods described above in fertilized and adjacent control plots. I made ANPP measurements in fertilized and control plots in late August 2007 (*Bromus tectorum* estimates taken in early June) using the methods described above.

Statistical Analyses

I conducted both microsite (between/under perennial grasses) and field-scale analyses of plant and soil characteristics. I calculated field-scale characteristics by weighting each microsite measurement according to the proportional cover of each microsite (Vinton and Burke 1995). I multiplied the average value for a plant or soil characteristic under perennial grasses in each field by the proportional vegetation basal cover, and multiplied the average value for between perennial grasses in each field by the proportional basal cover of bare ground in each field, and summed the two values. Field scale characteristics for early CRP fields seeded with native perennial grasses were calculated using only between perennial grass measurements because no perennial grasses had established in the field.

For microsite analyses, I performed analysis of variance (ANOVA) on plant and soil characteristics with field type and microsite as the main effects (Proc GLM, SAS 9.2, SAS Institute Inc. 2002-2007, Cary, NC, USA). I used a Tukey multiple comparison adjustment when comparing among field types for each microsite. For field-scale analyses, field type was used as the main effect. For nitrogen additions, nitrogen treatment was an additional main effect. I performed repeated measures ANOVA on inorganic nitrogen since it was measured in multiple years, with year as the repeated measure modeled in an autoregressive correlation structure (Proc Mixed, SAS 9.2). Regression was performed to explain relationships between vegetation and soil characteristics and the relationships among different soil characteristics (Proc Reg, SAS 9.2).

Results

Carbon in aboveground net primary production (ANPP-C) in CRP fields ranged from 32.7-55.1 g C m^{-2} (Table 1). Mid and late CRP fields had significantly higher ANPP-C than early CRP fields. ANPP-C was not significantly different between late CRP fields seeded with native and introduced perennial grasses, but there was nearly twice as much ANPP-C in mid and late CRP fields as undisturbed shortgrass steppe. Nitrogen in ANPP (ANPP-N) in CRP fields ranged from 0.8-1.3 g N m^{-2} (Table 1). There was significantly more ANPP-N in mid compared to early CRP fields, but no other significant differences among CRP fields or between CRP fields and undisturbed shortgrass steppe.

Carbon in belowground net primary production (BNPP-C) between perennial grasses was also higher in mid and late CRP fields relative to early CRP fields along the chronosequence (not significant; Fig. 1). There were no significant differences in BNPP-C between perennial grasses in late CRP fields seeded with native compared to introduced perennial grasses. Undisturbed shortgrass steppe had the highest BNPP-C between perennial grasses. BNPP-C under perennial grasses in CRP fields ranged from 57-110 g C m^{-2} and was not significantly different between mid and late CRP fields seeded with native perennial grasses. However, BNPP-C under perennial grasses was significantly lower in late CRP fields seeded with introduced perennial grasses than mid CRP fields seeded with native perennial grasses and undisturbed shortgrass steppe. There were significant differences in BNPP-C between and under perennial grasses in mid and late CRP fields seeded with native perennial grasses and undisturbed shortgrass steppe, but not CRP fields seed with introduced perennial grasses. At the field scale, BNPP-C significantly increased by 31 g C m^{-2} between early and late CRP fields seeded with native perennial grasses (Table 1). BNPP-C in late CRP fields seeded with native perennial grasses was 10 g C m^{-2} higher compared to introduced perennial grasses, but this difference was not significant. There was significantly higher BNPP-C in undisturbed shortgrass steppe relative to all CRP fields.

There were no significant differences in nitrogen in BNPP (BNPP-N) both between and under perennial grasses among CRP fields, but there was significantly higher BNPP-N at both microsites in undisturbed shortgrass steppe compared to all CRP fields (Fig. 2). BNPP-N under perennial grasses in CRP fields ranged from 0.9-1.3 g N m^{-2} compared to 2.9 g N m^{-2} in undisturbed shortgrass steppe. BNPP-N was significantly higher under than between perennial grasses in mid and late CRP fields seeded with native perennial grasses and undisturbed shortgrass steppe. At the field scale, there was a moderate increase in BNPP-N of 0.4 g N m^{-2} between early and late CRP fields seeded with native perennial grasses (not significant; Table 1). BNPP-N in undisturbed shortgrass steppe was nearly three times greater than any CRP field.

Soil bulk density was significantly higher in early CRP fields seeded with native perennial grasses than all other CRP fields and undisturbed shortgrass steppe (Table 2). Bulk density was significantly higher between perennial grasses than under perennial grasses in all CRP fields and undisturbed shortgrass steppe. There were no significant differences in soil texture among CRP fields or between CRP fields and undisturbed shortgrass steppe (Table 2). There was a trend for decreasing sand content and increasing silt and clay content along the chronosequence (not significant).

Total soil organic carbon (SOC) and soil nitrogen (SN) were highly correlated ($r = 0.96$, $P < 0.0001$) and differences among field types in each of the two pools were related. Total SOC losses (Fig. 3a) due to cropping practices were between 30-50% (45% at the field scale; Table 1) and total SN losses (Fig. 4a) were 30-45% (39% at the field scale; Table 1), depending on which microsite in the undisturbed shortgrass steppe they were compared. There was no change in total SOC or SN between perennial grasses along the chronosequence, but total SOC increased under perennial grasses between mid and late CRP fields by 200 g C m^{-2} and total SN increased 14 g N m^{-2}. There were no significant differences in total SOC or SN between late CRP fields seeded with native and introduced perennial grasses at either microsite. However, there was a trend of more total SOC under native compared to introduced perennial grasses. Undisturbed shortgrass steppe had significantly higher total SOC and SN under perennial grasses than all CRP fields except late fields seeded with native perennial grasses. There were significant microsite differences in total SOC and SN between and under perennial grasses in undisturbed shortgrass steppe and late CRP fields seeded with native perennial grasses. There were also significant microsite differences in total SOC in late fields seeded with *Agropyron intermedium*. At the field scale, total SOC and SN increased by 30 g C m^{-2} and 4 g N m^{-2} between early and late CRP fields in the chronosequence (not significant; Table 1). There was higher total SOC and SN in CRP fields seeded with native compared to introduced perennial grasses, but these differences were not significant. Total SOC and SN were significantly higher in undisturbed shortgrass steppe compared to all CRP fields.

SOC in the fine and coarse fractions had patterns similar to total SOC across field types, except there were no microsite differences in late CRP fields seeded with *Agropyron intermedium* (Fig. 3b). SN in the coarse fraction had patterns similar to total SN (Fig. 4b). SN in the fine fraction differed from total SN because it was significantly higher between plants in undisturbed shortgrass steppe than early CRP fields, was significantly lower in early compared to late CRP fields, and was significantly higher in late CRP fields seeded with native perennial grasses than introduced perennial grasses. Clay content explained some of the variability in total SOC ($r^2 = 0.27$, $P = 0.002$) and total SN ($r^2 = 0.28$, $P = 0.004$). SOC and SN associated with clay (total – POM fractions) comprised 60-90% of the total.

Inorganic N significantly increased between plants along the chronosequence in 2005, but not in subsequent years (Fig. 5). There were no significant differences in inorganic N at this microsite between late CRP fields seeded with native and introduced perennial grasses in all years. Undisturbed shortgrass steppe had significantly higher inorganic N between perennial grasses than all CRP fields in all years except late fields seeded with native perennial grasses in 2005 and 2007. There were no significant differences in inorganic N under perennial grasses between mid and late CRP fields in the chronosequence and between native and introduced perennial grasses in late CRP fields. Undisturbed shortgrass steppe had significantly higher inorganic N under perennial grasses than all CRP fields in 2006 and 2007 except late fields seeded with *Agropyron intermedium.* Inorganic N was generally higher under compared to between perennial grasses in most CRP fields and undisturbed shortgrass steppe, but only significantly in mid CRP fields seeded with native perennial grasses and late fields seeded with *Agryopyron intermedium.* At the field scale, inorganic N increased by as much as six times between early and late CRP fields, but these differences were not significant due to high within field variability (Table 1). There were no significant differences between late CRP fields seeded with native and introduced perennial grasses. Undisturbed shortgrass steppe had higher inorganic N than most CRP fields in all years except for late CRP fields in 2005.

Baseline soil respiration rates were ~ 0.03 g C m^{-2} h^{-1} in mid and late CRP fields in the chronosequence and undisturbed shortgrass steppe (Fig. 6). Soil respiration increased in all fields with 10 mm precipitation addition, and maximum rates were nearly twice as high in early CRP fields (0.39 g C m^{-2} h^{-1}) compared to late CRP fields (0.21 g C m^{-2} h^{-1}) and undisturbed shortgrass steppe (0.22 g C m^{-2} h^{-1}).

Soil respiration in control plots for the nitrogen addition experiment was similar to baseline measurements (Fig. 7). Nitrogen addition significantly increased soil respiration rate in early CRP fields and undisturbed shortgrass steppe, but not in late CRP fields. Early CRP fields that were fertilized had significantly higher respiration rates than late CRP fields that were fertilized. There were no significant differences in ANPP-C among CRP fields and undisturbed shortgrass steppe in control plots (Fig. 8). Nitrogen addition only affected ANPP-C in early CRP fields, where it was significantly higher than late CRP fields and undisturbed shortgrass steppe.

Discussion

An increase of NPP-C in mid and late CRP fields compared to early CRP fields demonstrates higher carbon input to SOC with increasing field age. This increase in NPP-C corresponded to an increase in perennial grasses (Chapter 3), which allocate more production below- than aboveground (Sims and Singh 1978). Therefore, belowground NPP-C (BNPP-C) under perennial grasses contributed the most to carbon input (Hook et al. 1991). No significant change in BNPP-C between mid and late CRP fields indicates that increased longevity of perennial grasses did not result in increased carbon input. However, an increase in basal cover of vegetation along the chronosequence (from 9.4% in early to 22.3% in late CRP fields) increased the proportion of the field with high BNPP-C. This resulted in an increase of BNPP-C at the field scale at a rate of 1.7 g C m^{-2} y^{-1}.

Carbon in aboveground NPP (ANPP-C) was twice as high in late CRP fields compared to undisturbed shortgrass steppe. High ANPP-C in CRP fields leads to high aboveground litter (Chapter 3), which may have a slow decomposition rate (Bontti et al., in press) and a gradual transition into SOC (Melillo et al. 1989) relative to belowground litter. High ANPP-C in CRP fields was compensated by low BNPP-C. BNPP-C was 15-30% lower (not significantly lower) in mid and late fields under native perennial grasses and more than 50% lower in fields under introduced perennial grasses relative to under perennial grasses in undisturbed shortgrass steppe. Low belowground C input, especially in CRP fields seeded with introduced perennial grasses, limits SOC recovery potential. Lower belowground carbon input from introduced compared to native perennial grasses is consistent with other studies (Christian and Wilson 1999, Ogle et al. 2004).

Nitrogen is tightly coupled with carbon in plant tissue (Asner et al. 1997), and similarly to ANPP-C, ANPP-N increased between early and mid CRP fields. The differences in BNPP-C among CRP fields did not exist in BNPP-N, largely due to the high C:N ratio in belowground tissue of native perennial grasses. Low belowground tissue quality can slow decomposition rate (Wedin and Tilman 1990, Janssen 1996), but may lead to larger amounts of soil organic carbon storage (Murphy et al. 2002). BNPP-N under perennial grasses coupled with increasing vegetation basal cover contributed to a trend of increasing BNPP-N at the field scale along the chronosequence of 0.02 g N m^{-2} y^{-1}. BNPP-N was much higher between and under perennial grasses in undisturbed shortgrass steppe relative to all CRP fields due to high BNPP and high percent nitrogen content in BNPP of perennial grasses in undisturbed shortgrass steppe.

There were differences in BNPP-C and BNPP-N at the microsite scale in CRP fields with caespitose, but not rhizomatous grasses. This small scale heterogeneity exists because the roots of most caespitose grasses, including *Bouteloua gracilis*, are found directly under or within 5 cm from edge of the plant (Coffin and Lauenroth

1991). In contrast, rhizomes can spread a greater horizontal distance from the edge of the plant.

I cannot be certain that all CRP fields had the same amount of total SOC and SN at the time of enrollment. Differences in cropping practices, duration of cropping, and other site conditions may have contributed to variability in initial SOC and SN in CRP fields. However, I am certain that all fields were influenced by long-term wheat-fallow cropping and had a similar amount of SOC and SN between perennial grasses, which increases the likelihood that CRP fields had similar initial amounts of SOC and SN. Total SOC and SN decreases due to cropping practices were within the variability of past estimates for this region of 20-50% (Haas et al. 1957, Tiessen et al. 1982, Schimel et al. 1985, Aguilar et al. 1988, Burke et al. 1989). Since SOC and SN estimates were made at the soil surface (0-5 cm), some of the decreases could be attributed to vertical redistribution of C and N in the soil profile during tillage practices, which is different than mechanisms leading to losses from the soil (Reeder et al. 1998).

Total SOC was positively correlated to BNPP-C across CRP field types and undisturbed shortgrass steppe ($r = 0.71$, $P < 0.0001$), a relationship consistent with previous findings (Gill et al. 1999). Since a majority of the BNPP-C was under perennial grasses, this microsite is where SOC storage occurred. Assuming similar initial SOC and SN in CRP fields, no significant carbon accrual occurred prior to perennial grass establishment, when BNPP-C was low. This supports the idea that SOC in CRP fields, like other grasslands is controlled by perennial grass root dynamics (Anderson and Coleman 1985, Dormaar 1992). A rate of increase of 22 g

C m^{-2} y^{-1} under perennial grasses between mid and late CRP fields is much higher than previously documented for this region (Burke et al. 1995) and suggests that substantial recovery is possible at the plant scale. However, these changes in SOC after perennial grass establishment were lower at the field scale (7.8 g C m^{-2} y^{-1}) and even lower across the entire chronosequence (1.6 g C m^{-2} y^{-1}). This rate of increase is lower than rates of 40-60 g C m^{-2} y^{-1} in more mesic grasslands (Lal et al. 1999, McLaughlan et al. 2006, Matamala et al. 2008). Carbon storage was low in CRP fields compared to undisturbed shortgrass steppe at the field scale. Even after 18 years of recovery, late CRP fields seeded with native perennial grasses had 40% less total SOC than undisturbed shortgrass steppe. A major limitation to recovery is low vegetation basal cover in CRP fields relative to undisturbed shortgrass steppe, which limits the spatial extent of root growth. Lower BNPP-C in CRP fields under introduced compared to native perennial grasses lead to more than 100 g C m^{-2} difference in SOC (not significant). With a longer recovery time, this difference in SOC may become more pronounced.

The strong correlation between total SOC and SN supports the close linkage between the carbon and nitrogen cycles in the soil. Similar to carbon cycling, total SN was positively correlated to BNPP-N across CRP field types and undisturbed shortgrass steppe ($r = 0.84$, $P < 0.0001$). Since the nitrogen cycle is relatively closed between the soil and vegetation (Rosswall 1976), it is more difficult to determine the mechanism by which total SN increased at the field scale along the CRP chronosequence at a rate of 0.2 g N m^{-2} y^{-1}. Potential mechanisms include increased input through nitrogen fixation, redistribution of the soil profile, or atmospheric deposition (Knops and Tilman 2000). Symbiotic nitrogen fixation was likely low in CRP fields due to < 1% canopy cover of legumes in CRP fields and undisturbed shortgrass steppe (Chapter 2), and most redistribution of the soil profile occurs during tillage and is minimal during CRP enrollment.. Atmospheric deposition estimates in the shortgrass steppe region are ~ 0.5 g N m^{-2} y^{-1} (NADP 2007), which is higher than the rate of total SN increase in CRP fields. This increases the likelihood that changes in SN were influenced by outputs through leaching and volatization. SN may have increased along the chronosequence because it progressively became tied up in plant biomass and soil organic matter, reducing its potential to be lost from the system (Conant et al. 2005).

Differences in total SOC and SN at the microsite scale in undisturbed shortgrass steppe and late CRP fields seeded with native perennial grasses are consistent with heterogeneity of BNPP in these field types. Belowground litter, which accumulates from BNPP, contributes to high total SOC and SN under perennial grasses (Hook et al. 1991). Aboveground litter, physical erosion and deposition from between to under perennial grasses also contribute to this pattern (Burke et al. 1998). The microsite differences in total SOC that existed in CRP fields seeded with *Agropyron intermedium*, a rhizomatous perennial grass is contradictory to previous findings (Derner and Briske 2001). High basal area of *Agropyron intermedium* ramets and noticeable accumulation of aboveground litter (personal observations) under clones may have contributed to this heterogeneity.

Carbon and nitrogen in the coarse POM fraction represent pools with an intermediate turnover (Cambardella and Elliott 1992), but more recent plant inputs than fine POM (Kelly et al. 1996). This fraction had patterns across field types similar to total SOC and SN, suggesting that much of the recovery in carbon and nitrogen storage could be associated with a pool with relatively short turnover time (< 20 years; Kelly et al. 1996, Gill et al. 1999). A significantly lower C:N ratio in fine relative to coarse POM across field types ($t = 31.55$, $P < 0.0001$) supports the idea that this fraction represents a later stage of decomposition, which is chemically and physically more resistant and has a slower turnover time than coarse POM (Kelly et al. 1996). There was little recovery of carbon and nitrogen in fine POM in mid relative to early CRP fields. This supports earlier work by Robles and Burke (1998) in CRP fields of comparable age at a site near this study and their conclusion that the turnover time of the fine POM pool is longer than the short time perennial grasses have been established in fields. However, late CRP fields seeded with native perennial grasses had double the carbon and nitrogen in the fine POM fraction compared to mid CRP fields. There were also significant microsite differences in these fields, which collectively indicate native perennial grasses have contributed to the formation of a more recalcitrant form of organic matter. This recovery was faster than expected given the long turnover time of this pool (> 20 years; Kelly et al. 1996, Gill et al. 1999). However, some recovery may be possible if C and N inputs from plants become quickly stabilized in soils (McLaughlan et al. 2006). Alternatively, the formation of fine POM could be faster than expected because native perennial grasses had relatively low root tissue quality (high C:N ratio) and may have had more lignin, which contributed to the formation of recalcitrant SOM (Paustian et al. 1992). This increase of fine POM occurred at the soil surface, where accumulation is most likely to occur (Gill et al. 1999). Recovery of recalcitrant soil organic carbon is important because it contributes more to the long-term storage of carbon than active pools, which quickly turnover C back into the atmosphere (Hungate et al. 1997).

Soil physical characteristics had an important influence on the abundance of SOC and SN. A large percentage of total SOC and SN was associated with clay in CRP fields due to the physical and chemical stability provided by mineral organic binding (Tisdall and Oades 1982). Differences in clay content among fields and along the chronosequence explained some of the variability of SOC and SN. Bulk density was also associated with SOC and SN. Early CRP fields had higher than expected total SOC and SN because there was a greater mass of surface soil at these compacted sites (Murty et al. 2002). This resulted in a 2% decrease of total SOC and SN on an area basis (g m^{-2}) at the field scale between early and mid CRP fields. However, after accounting for differences in bulk density, there was an 18% increase in total SOC and 29% increase in total SN on a mass basis (g kg^{-1}) between these fields. The reduction in bulk density that occurred between mid and late CRP fields was likely due to increased soil aggregate formation associated with the presence of roots (Elliott 1986).

Inorganic N is a relatively small proportion of total SN (Post et al. 1985), which is biologically available and determined by the mineralization of soil organic N. The increase of in situ inorganic N along the chronosequence, especially under perennial grasses was related to an increase in total SN. Although I did not measure soil organic N directly, the largest pool of total SN was organic. A positive correlation between inorganic N and total SN in all years ($r = 0.46$, $P < 0.0001$)

supports the linkage between organic and inorganic N. An increase in inorganic N along the chronosequence is consistent with other studies (Burke et al. 1995, Reeder et al. 1998) and demonstrates improved nutrient availability through conversion to perennial grassland. In contrast, inorganic N decreased as field age increased in mesic grassland chronosequences (Baer et al. 2002, Camill et al. 2004). Since resin bags compete for inorganic N with plants and microbes, the discrepancy is likely due to high rates of nitrogen immobilization and plant uptake at the mesic site (Barrett and Burke 2002). The quantity and quality of plant litter also regulates N mineralization (Wedin and Tilman 1990), with high quantity and quality of litter inputs causing high mineralization rates. BNPP-N was positively correlated ($r = 0.56$, $P < 0.0001$), while the C:N ratio of belowground plant tissue was negatively correlated ($r = 0.42$, $P < 0.0001$) to inorganic nitrogen across all years. Since the quantity and quality of belowground plant inputs was highest in undisturbed shortgrass steppe relative to all CRP fields, this is where there was the highest nitrogen mineralization. Inorganic N was also positively correlated to the amount of precipitation that occurred while the resin bag was in the soil each year ($r = 0.33$, $P = 0.001$). Water availability likely affected inorganic nitrogen through its control of N mineralization rate and its influence on ion transport to the resin bags (Binkley 1984).

Carbon is closely linked to nitrogen in organic pools, but becomes decoupled as it is respired as CO_2. Respiration losses are important because they influence the size and turnover of SOC in recovering CRP fields (Raich and Schlesinger 1992). Baseline soil respiration measurements revealed that early and late CRP fields were not significantly different from each other or undisturbed shortgrass steppe in potential carbon losses. This implies that the high respiration rates associated with tillage practices may have decreased in CRP fields. However, maximum respiration rates that occurred with water addition were almost twice as high in early CRP fields compared to undisturbed shortgrass steppe. Possible explanations for higher maximum respiration rates in these fields include a lack of soil aggregate recovery (Elliott 1986), which leaves labile SOC exposed, or high quantity and quality of aboveground litter from annual plants that dominate this field (Chapter 2). These maximum respiration rates are not likely to be sustained over the long-term, but represent the potential for short-term carbon loss during periods when water availability does not limit respiration. This potential could mean that low C inputs in early CRP fields may be rapidly lost through respiration, which may help explain low SOC accrual between early and mid CRP fields. It also suggests that early CRP fields may serve as a source, rather than a sink, for atmospheric carbon.

Nitrogen cycling affects carbon storage (Van Cleve and Powers 1995). One example of this is that human-induced N fertilization may lead to increased C storage (Schlesinger and Andrews 2000). N availability influences C storage through its influence on NPP. Although the internal recycling of N may meet the requirements for NPP in CRP fields, N availability can be low and limit NPP (Vitousek and Howarth 1991). This was the case in early CRP fields, where inorganic N was low and additional N doubled ANPP-C. Fast growing annual species in these fields rapidly utilized the nitrogen to increase photosynthesis, and consequently production, which can lead to higher C input into SOC. Slower growing perennial grasses had high nutrient use efficiency (Vitousek 1982) and did not respond to increased inorganic N over the growing season. Nitrogen availability can also affect carbon storage through its effect on C efflux. Nitrogen fertilization increased the soil respiration rate of early CRP fields and undisturbed shortgrass steppe, which reduces SOC storage. Additional nitrogen likely had effects on microbial metabolism and decomposition, but the effects of N fertilization on soil C turnover are complex (Neff et al. 2002) and depend on substrate chemistry (Knorr et al. 2005, Hobbie 2008). Additional N may have increased decomposition of labile SOC during the study and increased carbon in microbial biomass, which turns over rapidly, but may eventually increase SOC with slower turnover times (Barrett and Burke 2002), which leads to slow decomposition rate (Berg and Matzner 1997). Longer-term effects may also include feedbacks between high plant litter quality and accelerated decomposition (Vinton and Burke 1995, Bontti et al., in press). High respiration rate in early CRP fields due to nitrogen addition may counter-balance any of the effects that lead to increased SOC storage.

The capacity of soil to offset anthropogenic sources of carbon (Lal 2004) is largely determined by land use. The net balance of NPP inputs and respiration outputs determines SOC storage in CRP fields. These fluxes and SOC were influenced by time since CRP enrollment and seed mix. No significant carbon accrual occurred prior to perennial grass establishment, when NPP-C was low and potential respiration losses were high. The increased dominance of perennial grasses in CRP fields led to an increase in NPP-C along the chronosequence, which increased total SOC by as much as 22 g C m^{-2} y^{-1} and may have contributed to the formation of recalcitrant SOC after 18 years. However, the carbon storage resulting from this increase in total SOC was not statistically significant at the field scale due to low vegetation basal cover in CRP fields and was only 4% of the total SOC in undisturbed shortgrass steppe. Low BNPP-C under introduced compared to native perennial grasses led to relatively low SOC and less small scale (microsite) heterogeneity. Nitrogen (N) was linked to BNPP-C and SOC and recycled between vegetation and soil. N availability could largely be explained by increases in soil organic nitrogen, but was also related to belowground tissue quality and precipitation. Increases in N availability may have effects on carbon storage, especially in early CRP fields.

Literature Cited

Aguilar, R., E.F. Kelly, and R.D. Heil. 1988. Effects of cultivation on soils in northern Great Plains rangelands. Soil Science Society of America Journal 52: 1081-1085.

Amundson, R. 2001. The Soil Carbon Cycle. Annual Reviews of Earth and Planetary Sciences 29: 535-562.

Anderson, D.W., and D.C. Coleman. 1985. The dynamics of soil organic matter in grassland soils. Journal of Soil and Water Conservation 40: 211-216.

Asner, G.P., T.R. Seastedt, and A.R. Townsend. 1997. The decoupling of terrestrial carbon and nitrogen cycles. Bioscience 47: 226-234.

Baer, S.G., C.W. Rice, and J.M. Blair. 2000. Assessment of soil quality in fields with short and long term enrollment in the CRP. Journal of Soil and Water Conservation 55: 142-145.

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12: 1688-1701.

Barrett, J.E., and I.C. Burke. 2002. Nitrogen retention in semiarid ecosystems across a soil organic-matter gradient. Ecological Applications 12: 878-890.

Berg, B., and E. Matzner. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Reviews 5:1–25.

Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Science Society of Americal Journal 47: 1050-1052.

Binkley, D. 1984. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Science Society of America Journal 48: 1181-1184.

Bontti, E.E., J.P. DeCant, S.M. Munson, M. Gathany, A. Przeszlowska, M.L. Haddix, I.C. Burke, W.J. Parton, and M.E. Harmon. In Press. Litter decomposition in grasslands of Central North America (US Great Plains). Global Change Biology.

Breuer, L., J.A. Huisman, T. Keller, and H.G. Frede. 2006. Impact of a conversion from cropland to grassland on C and N storage and related soil properties: analysis of a 60-year chronosequence. Geoderma 133: 6-18.

Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989.

Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Science Society of America Journal 53: 800-805.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program. Ecological Applications 5: 793–801.

Burke, I.C., W.K. Lauenroth, M.A. Vinton, P.B. Hook, R.H. Kelly, H.E. Epstein, M.R. Aguiar, M.D. Robles, M.O. Aguilera, K.L. Murphy, and R.A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42: 121-143.

Burke, I.C., A.R. Mosier, P.B. Hook, D.G. Milchunas, J.E. Barrett, M.A. Vinton, R.L. McCulley, J.P. Kaye, R.A. Gill, H.E. Epstein, R.H. Kelly, W.J. Parton, C.M. Yonker, P. Lowe, and W.K. Lauenroth. 2008. Soil organic matter and nutrient dynamics of shortgrass steppe ecosystems. Pages 306-341 *in* W.K. Lauenroth and I.C. Burke, eds. Ecology of the shortgrass steppe. Oxford University Press, New York.

Cambardella, C.A., and E.T. Elliott. 1992. Particulate soil organic matter changes across a grassland cultivation sequence. Soil Science Society of America Journal 56: 777-783.

Camill, P., M.J. McKone, S.T. Sturges, W.J. Severud, E. Ellis, J. Limmer, C.B. Martin, R.T. Navartil, A.J. Purdie, B.S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14: 1680-1694.

Christian, J.M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. Ecology 80: 2397-2407.

Coffin, D. P., and W. K. Lauenroth. 1991. Effects of competition on spatial distribution of roots of blue grama. Journal of Range Management 44: 67-70.

Coffin, D.P, W.K. Lauenroth, and I.C. Burke 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications 6: 538-555.

Cole, C.V., J. Duxbury, J. Freney, O. Heinemeyer, K. Minami, A. Mosier, K. Paustian, N. Rosenberg, N. Sampson, D. Sauerbeck, and Q. Zhao. 1997. Global estimates of potential mitigation of greenhouse gas emissions by agriculture. Nutrient Cycling in Agroecosystems 49: 221-228.

Conant, R.T., K. Paustian, and E.T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11: 343-355.

Conant, R.T., K. Paustian, S.J. Del Grosso, and W.J. Parton. 2005. Nitrogen pools and fluxes in grassland soils sequestering carbon. Nutrient Cycling in Agroecosystems 71: 239-248.

Day, P.R. 1965. Soil texture. *In* C.L. Black, ed. Methods of soil analysis. Part 2. Agronomy 9: 545-567.

Diaz, S., J.P. Grime, J. Harris, and E. McPherson. 1993. Evidence of a feedback mechanism limiting plant response to elevated CO_2. Nature 364: 616-617.

Derner, J.D., and D.D. Briske. 2001. Below-ground carbon and nitrogen accumulation in perennial grasses: A comparison of caespitose and rhizomatous growth forms. Plant and Soil 237: 117-127.

Dormaar, J.F. 1992. Decomposition as a natural process in grasslands. Pages 121-136 *in* Coupland RT, ed. Natural grasslands: Introduction and Western Hemisphere. Elsevier, New York.

Elliott, E.T. 1986. Aggregate structure and carbon, nitrogen, and phosphorous in native and cultivated soils. Soil Science Society of America Journal 50: 627-633.

Gill, R. A., I. C. Burke, D. G. Milchunas, and W. K. Lauenroth. 1999. Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. Ecosystems 2: 226–236.

Guo, L.B., and R.M. Gifford. 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Biology 8: 345-360.

Haas, H.J., C.E. Evans, and E.F. Miles. 1957. Nitrogen and carbon changes in Great Plains soils as influenced by cropping and soil treatments. I.S. Department of Agriculture Technical Bulletin 1164, U.S. Government Printing Office, Washington D.C.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138: 247-256.

Hobbie, S.E. 2008. Nitogen effects on decomposition: a five-year experiment in eight temperate sites. Ecology 89: 2633-2644.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1994. Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration gaps. Journal of Ecology 82: 485-494.

Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin III, H.A. Mooney, and C.B. Field. 1997. The fate of carbon in grasslands under carbon dioxide enrichment.

Nature 388: 576-579.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller, eds. Cambridge University Press, Cambridge and New York.

Janssen, B.H. 1996. Nitrogen mineralization in relation to C:N ratio and decomposability of organic materials. Plant and Soil 181: 39-45.

Jordan, C.F., and G. Escalante. 1980. Root productivity in an Amazonian rain forest. Ecology 61: 14-18.

Kelly, R.H., I.C. Burke, and W.K. Lauenroth. 1996. Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. Ecology 77: 2516-2527.

Knops, J.M.H., and D. Tilman. 2000. Dynamics of soil nitrogen and carbon for 61 years after agricultural abandonment. Ecology 81: 88–98.

Knorr, M., S. D. Frey, and P. S. Curtis. 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86: 3252–3257.

Kucharik, C.J., N.J. Fayram, and K.N. Cahill. 2006. A paired study of prairie carbon stocks, fluxes, and phenology: comparing the world's oldest prairie restoration with an adjacent remnant. Global Change Biology 12: 122-139.

Lal, R., R. F Follett, J. Kimble, and C. V. Cole. 1999. Managing U.S. cropland to sequester carbon in soil. Journal of Soil and Water Conservation 54: 374-381.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304: 1623-1627.

Lauenroth. W.K. 2008. Vegetation of the shortgrass steppe. In Lauenroth, W.K. and I.C. Burke, eds. Ecology of the shortgrass steppe. Oxford University Press, New York.

Lowe, P.N., W.K. Lauenroth, and I.C. Burke. 2002. Effects of nitrogen availability on the growth of native grasses and exotic weeds. Journal of Range Management 55: 94–98.

Matamala, R., J.D. Jastrow, R.M. Miller, and C.T. Garten. 2008. Temporal changes in C and N stocks of restored prairie: implications for C sequestaration strategies. Ecological Applications 18: 1470-1488.

McLauchlan, K.K., S.E. Hobbie, and W.M. Post. 2006. Conversion from agriculture to grasslands builds soil organic matter on decadal timescales. Ecological Applications 16: 143-153.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil 115: 189-198.

Munson, S.M., T.J. Benton, W.K. Lauenroth, and I.C. Burke. In Review. Soil respiration following pulse precipitation events in the shortgrass steppe. New Phytologist.

Murphy, K., I.C. Burke, M.A. Vinton, W.K. Lauenroth, M. Aguiar, D. Wedin, R.A. Virginia, and P.N. Lowe. 2002. Regional analysis of litter quality in the central grassland region of North America. Journal of Vegetation Science 13: 395–402.

Murty, D., M.U.F. Kirschbaum, R.E. Mcmurtrie, and H. Mcgilvray. 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. Global Change Biology 8: 105-123.

National Atmospheric and Deposition Program. 2007. Isopleth maps. 2 August 2008 from: http://nadp.sws.uiuc.edu/isopleths/maps2007

Natural Resources Conservation Service. 1991. Technical Guide, Section IV, Standards and Specifications, Range Seeding, Colorado. USDA, Colorado.

Natural Resource Conservation Service. 2008. Soil Survey. 2 August 2008 from: http://soils.usda.gov/survey

Neff, J.C., A.R. Townsend, G. Gleixner, S.J. Lehman, J. Turnbull, and W.D. Bowman. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419: 915-917.

Oades, J.M. 1988. The retention of organic matter in soils. Biogeochemistry 5: 35-70.

Odum, E.P. 1960. Organic production and turnover in old field succession. Ecology 41: 34-49.

Ogle, S.M., D.S. Ojima, and W.A. Reiners. 2004. Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. Biological Invasions 6: 365–377.

Parton W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173–1179.

Paul, E.A. 1984. Dynamics of organic matter in soils. Plant and Soil 76: 275-285.

Paustian, K., W. J. Parton, and J. Persson. 1992. Modeling soil organic matter in organic-amended and nitrogen-fertilized long-term plots. Soil Science Society of America Journal 56: 476–488.

Post, W.M., W.R. Emanuel, P.J. Zinke, and A.G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature 298: 156-159.

Post, W.M., J. Pastor, P.J. Zinke, and A.G. Stangenberger. 1985. Global patterns of soil nitrogen storage. Nature 317: 613-616.

Post, W.M., and K.C. Kwon. 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6: 317-327.

Raich, J.W., and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B: 81-99.

Reeder, J.D., G.E. Schuman, and R.A. Bowman. 1998. Soil C and N changes on conservation reserve program lands in the Central Great Plains. Soil and Tillage Research 47: 339-349.

Reeder, J.D., G.E. Schuman, J.A. Morgan, and D.R. Lecain. 2004. Response of organic and inorganic carbon to long-term grazing of the shortgrass steppe. Environmental Management 33: 485-495.

Robles, M.D., and I.C. Burke. 1997. Legume, grass, and Conservation Reserve Program effects on soil organic matter recovery. Ecological Applications 7: 345-357.

Robles, M.D., and I.C. Burke. 1998. Soil organic matter recovery on Conservation Reserve Program fields in Southeastern Wyoming. Soil Science Society of America Journal 62: 725-730.

Rosswall, T. 1976. The internal nitrogen cycle between microorganisms, vegetation and soil. Pages 157-167 *in* Svensson, B.H. and Soderlund, R., eds. Nitrogen, phosphorus and sulphur – Global Cycles. SCOPE Report 7. Ecogical Bulletin 22.

Sala, O.E., and W.K. Lauenroth. 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia 53: 301-304.

Schimel, D. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1: 77-91.

Schimel, D., D.C. Coleman, and K.A. Horton. 1985. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma 36: 201-214.

Schlesinger, W.H., and J.A. Andrews. 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48: 7-20.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. Journal of Ecology 66: 573-597.

Skold, M.D. 1989. Cropland retirement policies and their effects on land use in the Great Plains. Journal of Production Agriculture 2: 197-201.

Smucker, A.J.M., S.L. McBurney, and A.K. Srivastava. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agronomy Journal 74:500-503.

Stevens, P.R., and T.W. Walker. 1970. The chronosequence concept and soil formation. Quarterly Review of Biology 45: 333-350.

Tiessen, H., J.W.B. Stewart, and J.R. Bettany. 1982. Cultivation effects on the amounts and concentration of carbon, nitrogen, and phosphorous in grassland soils. Agronomy Journal 74: 831-835.

Tisdall, J.M., and J.M. Oades. 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33: 141–163.

USDA Farm Service Agency. 2008. U.S. Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 27 June 2008). 4 November 2008 from: http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM

Van Cleve, K., and R.F. Powers. 1995. Carbon, soil formation, and ecosystem development. Pages 155-200 *in* W.W. McFee and J.M. Kelly, eds. Soil carbon forms and functions in forest soils. Soil Science Society of America, Madison.

Vinton, M.A., and I.C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76: 1116-1133.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119: 553-572.

Vitousek, P.M., H.A. Mooney, J. Lubchenco, J.M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277: 494-499.

Vitousek, P.M., and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87-115.

Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433-441.

			Field Type			
	SGS	**Native - Early**	**Native - Mid**	**Native - Late**	**BRIN - Late**	**AGIN - Late**
ANPP-C	26.8 (4.2)^{a}	32.7 (2.9)^{a}	55.1 (0.9)^{b}	49.1 (4.3)^{b}	43.1 (4.3)^{b}	51.8 (4.2)^{b}
ANPP-N	0.8 (0.2)^{ab}	0.8 (0.1)^{a}	1.3 (0.3)^{b}	1.2 (0.3)^{b}	0.8 (0.2)^{ab}	0.9 (0.1)^{ab}
BNPP-C	101.8 (12.0)^{a}	22.1 (3.2)^{b}	49.5 (7.7)^{bc}	52.6 (8.9)^{c}	39.3 (4.6)^{bc}	36.8 (4.2)^{bc}
BNPP-N	2.3 (0.3)^{a}	0.4 (0.1)^{b}	0.6 (0.2)^{b}	0.8 (0.2)^{b}	0.7 (0.0)^{b}	0.5 (0.1)^{b}
SOC	677.5 (106.0)^{a}	374.5 (24.3)^{b}	333.9 (25.4)^{b}	404.0 (39.0)^{b}	360.6 (20.4)^{b}	375.8 (20.4)^{b}
SN	67.5 (8.6)^{a}	41.5 (5.8)^{b}	40.6 (4.5)^{b}	45.5 (4.6)^{b}	44.1 (2.1)^{b}	43.0 (3.3)^{b}
N - 2005	21.3 (2.1)^{a}	2.3 (0.7)^{b}	7.2 (2.5)^{b}	14.9 (5.0)^{ab}	8.5 (3.7)^{ab}	13.5 (0.9)^{ab}
N - 2006	35.2 (9.9)^{a}	9.3 (2.2)^{b}	12.9 (1.8)^{b}	12.7 (1.2)^{b}	14.3 (3.2)^{b}	16.5 (0.4)^{b}
N - 2007	43.6 (6.6)^{a}	7.1 (0.7)^{b}	12.4 (0.7)^{b}	20.9 (6.7)^{b}	14.1 (7.0)^{b}	17.4 (2.3)^{b}

Table 1. Field scale estimates of carbon and nitrogen in above- (ANPP-C, ANPP-N) and belowground net primary production (BNPP-C, BNPP-N), total soil organic carbon (SOC), total soil nitrogen (SN), and inorganic nitrogen (N) in 2005, 2006, and 2007. Field scale estimates were made by weighting microsite estimates according to the proportion basal cover of each microsite within each field. Different letters within the same row indicate significant differences (Tukey adjusted $P < 0.05$) among field types.

				Field Type			
		SGS	**Native - Early**	**Native - Mid**	**Native - Late**	**BRIN - Late**	**AGIN - Late**
Bulk Density	*Between*	1.09 (0.03)*	**1.57 (0.01)**	1.21 (0.04)*	1.17 (0.03)*	1.18 (0.04)*	1.12 (0.08)*
	Under	1.00 (0.01)	.	1.10 (0.02)	1.09 (0.02)	1.06 (0.03)	1.04 (0.06)
Texture	*% Sand*	61.8 (8.9)	76.0 (1.8)	70.8 (3.5)	62.1 (7.4)	63.4 (3.0)	68.5 (1.9)
	% Clay	20.4 (4.6)	11.8 (0.5)	15.2 (0.7)	19.4 (7.7)	17.7 (2.5)	19.0 (2.1)
	% Silt	17.8 (5.1)	12.2 (2.2)	14.0 (2.8)	18.5 (0.3)	18.9 (4.2)	12.6 (0.5)

Table 2. Soil bulk density (g cm^{-3}) between and under perennial grasses and soil texture (%) (± standard error) in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN). **Bold** indicates that native-early fields had a significantly (Tukey adjusted $P < 0.05$) higher bulk density from all other field types and an asterisk (*) indicates significant difference ($P < 0.05$) between and under perennial grasses within a field type.

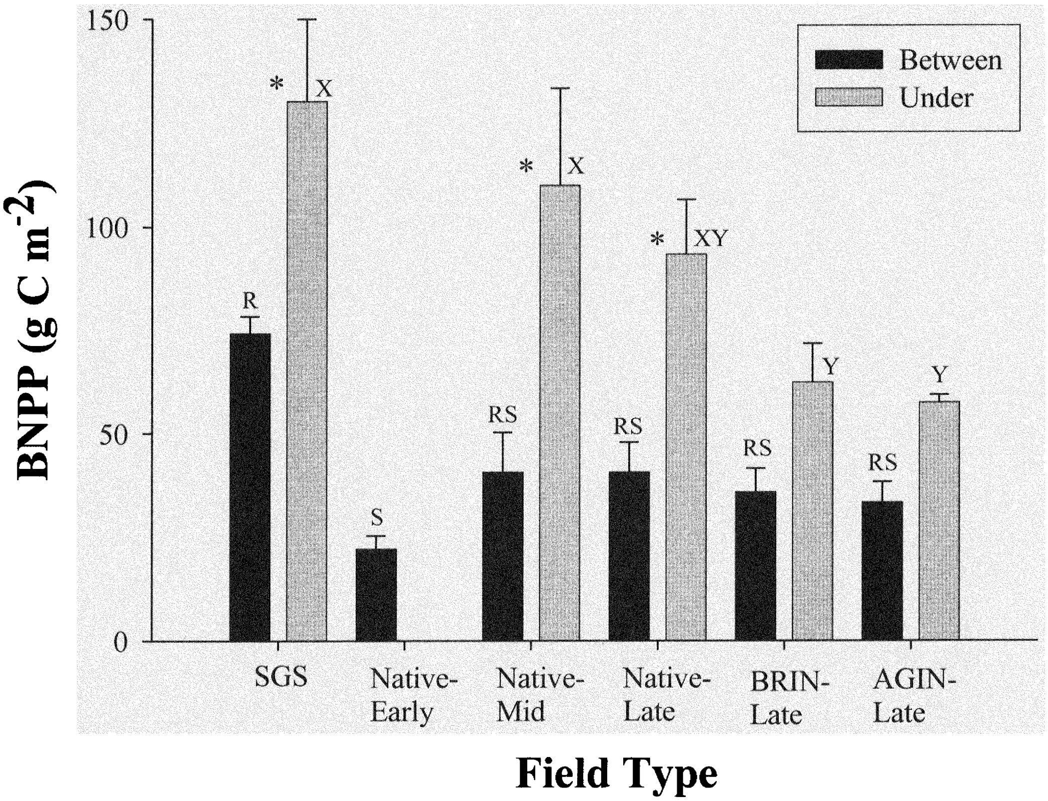

Figure 1. Carbon in belowground net primary production carbon (BNPP; ± SE) between and under perennial grasses in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN). Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in BNPP among field types and different asterices (*) designate significant ($P < 0.05$) differences in BNPP between and under perennial grasses.

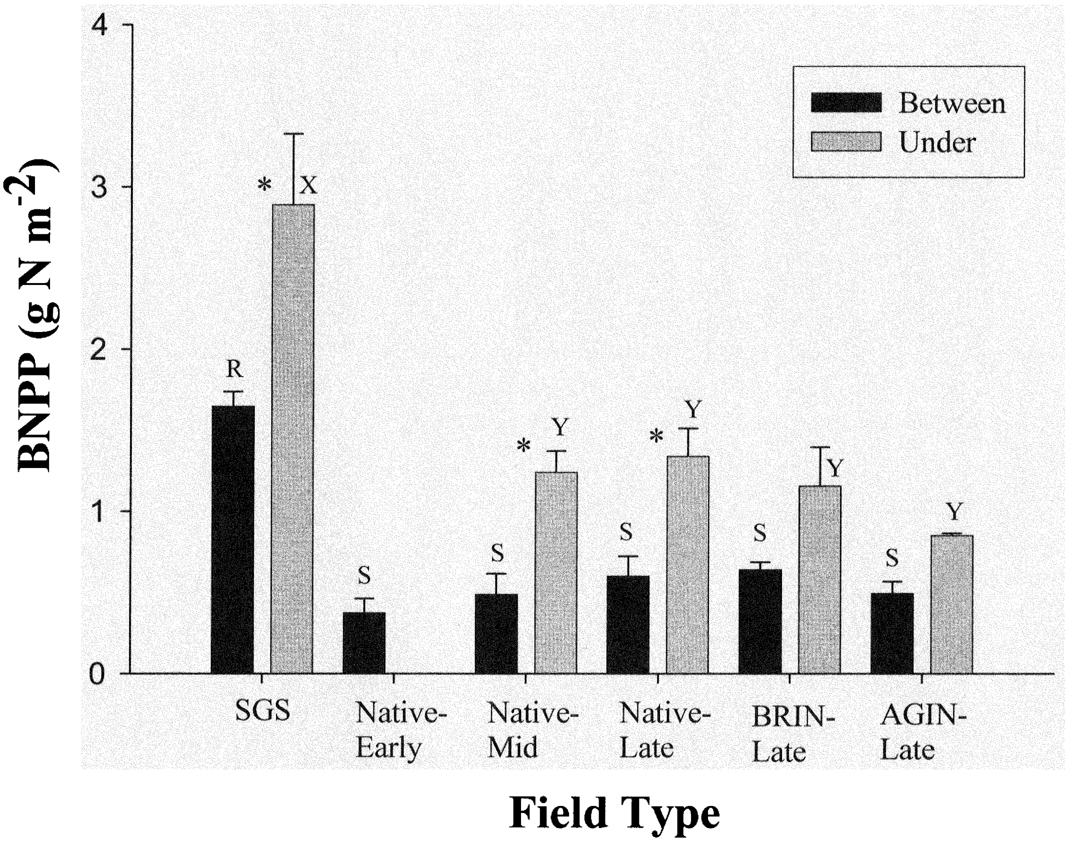

Figure 2. Nitrogen in belowground net primary production (BNPP; ± SE) between and under perennial grasses in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN). Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in BNPP among field types and different asterices (*) designate significant differences ($P < 0.05$) in BNPP between and under perennial grasses.

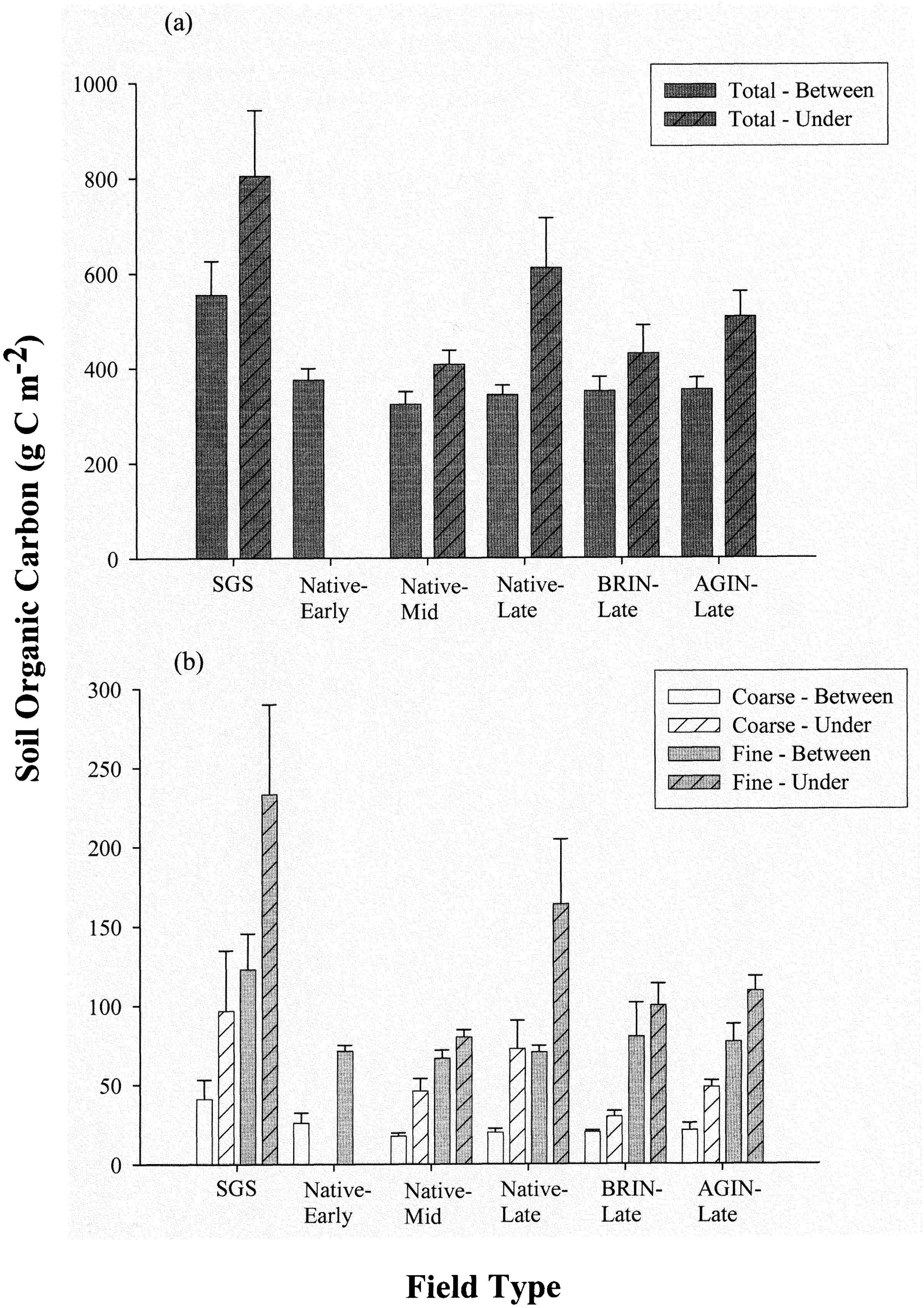
(a)
1000
800
600
400
200
0
Total - Between
Total - Under
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
(b)
300
250
200
150
100
50
0
Coarse - Between
Coarse - Under
Fine - Between
Fine - Under
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
Soil Organic Carbon (g C m^{-2})
Field Type

Figure 3. Total (a), coarse and fine (b) soil organic carbon (g C m^{-2}; ± SE) between and under perennial grasses in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN).

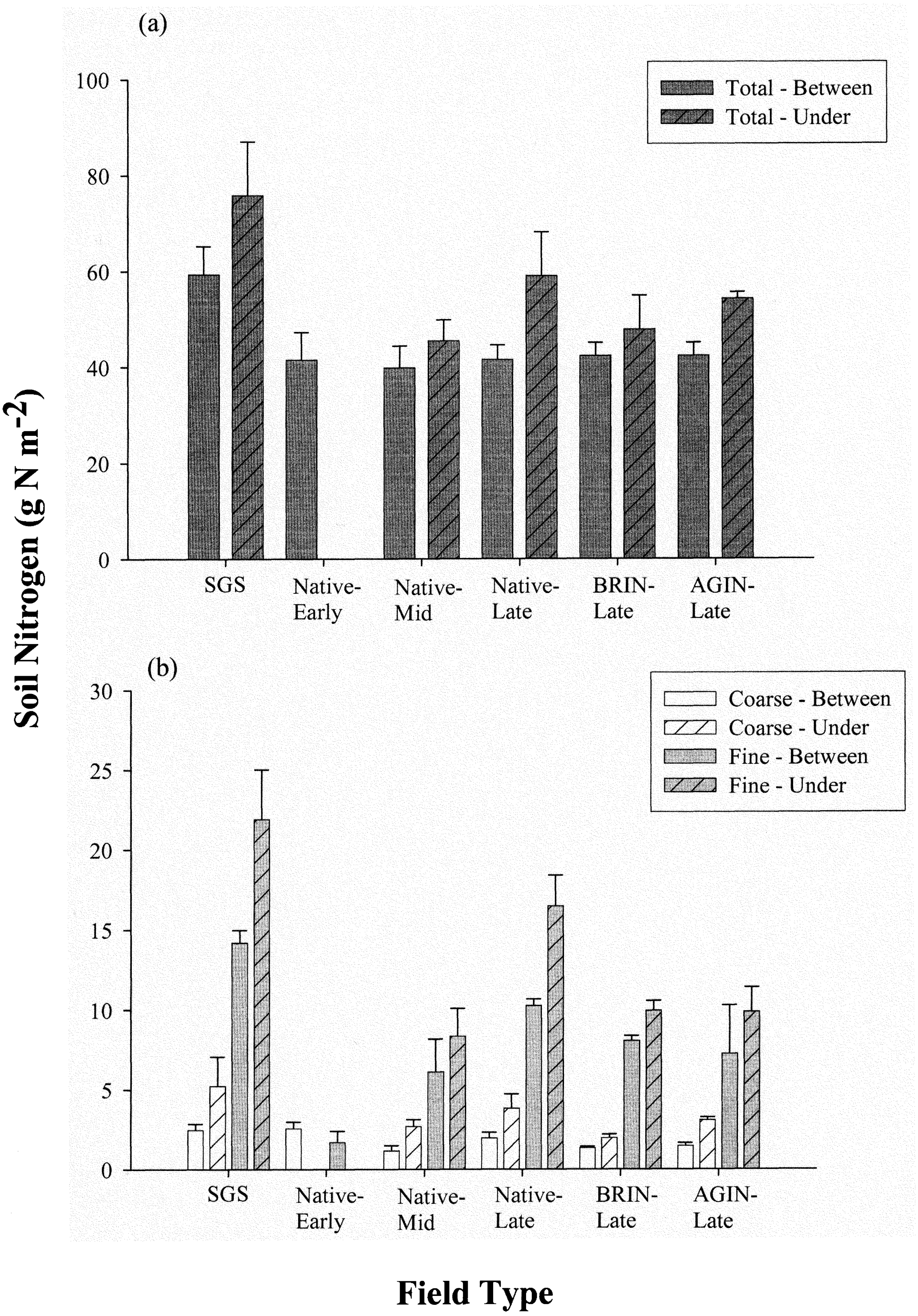
(a)
Total - Between
Total - Under
100
80
60
40
20
0
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
(b)
Coarse - Between
Coarse - Under
Fine - Between
Fine - Under
30
25
20
15
10
5
0
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
Soil Nitrogen (g N m-2)
Field Type

Figure 4. Total (a), coarse and fine (b) soil nitrogen (g N m^{-2}; ± SE) between and under perennial grasses in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN).

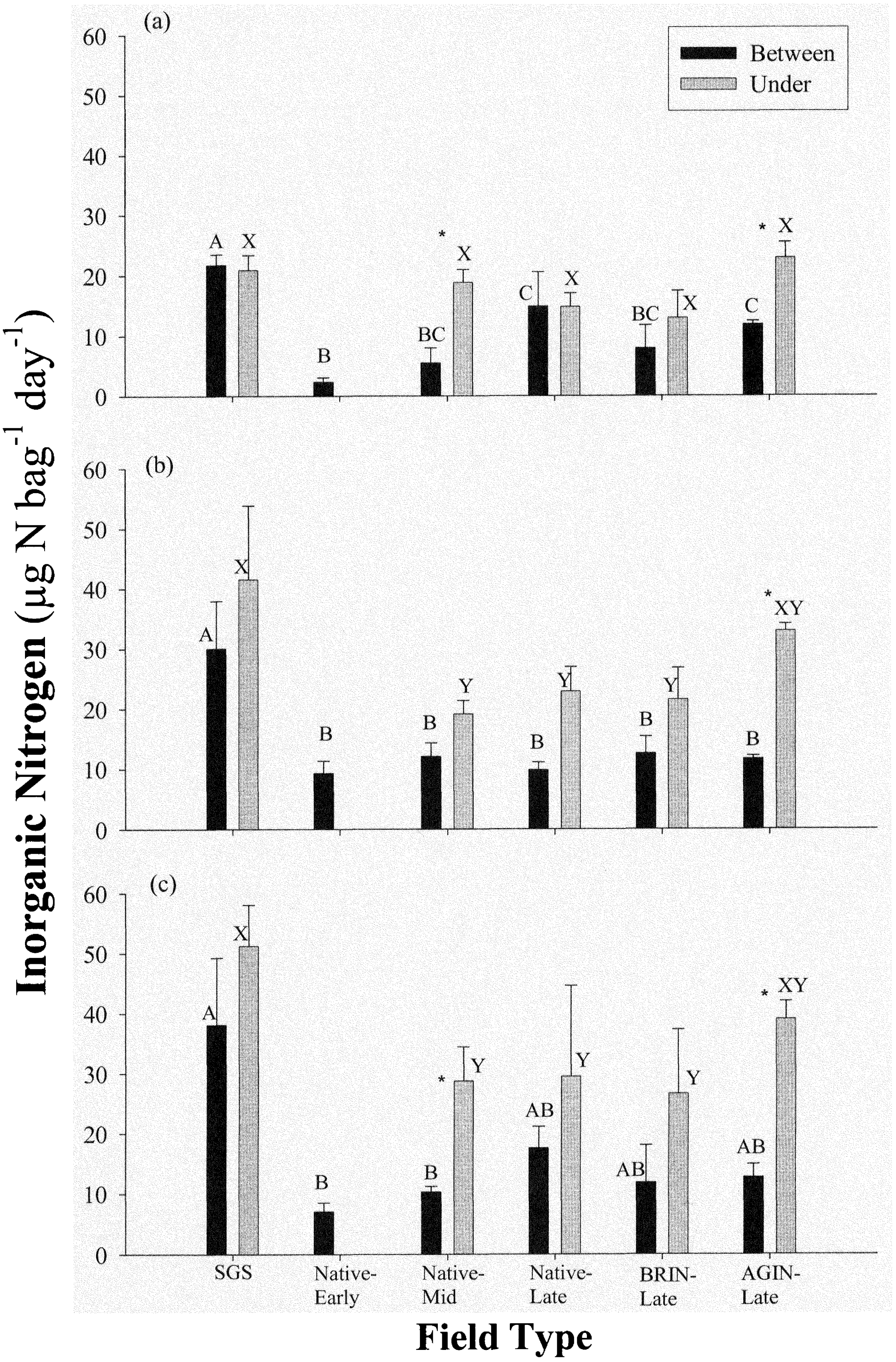
(a)
(b)
(c)
Between
Under
Inorganic Nitrogen (μg N bag⁻¹ day⁻¹)
0
10
20
30
40
50
60
A
X
B
BC
*
X
C
X
BC
X
C
*
X
A
X
B
B
Y
B
Y
B
Y
B
*
XY
A
X
B
B
*
Y
AB
Y
AB
Y
AB
*
XY
SGS
Native-Early
Native-Mid
Native-Late
BRIN-Late
AGIN-Late
Field Type

Figure 5. Inorganic nitrogen (nitrate and ammonium; ± SE) between and under perennial grasses in undisturbed shortgrass steppe (SGS), early, mid, and late CRP fields seeded with a native seed mix, and late CRP fields seeded with *Bromus inermis* (BRIN) and *Agropyron intermedium* (AGIN) in 2005 (a), 2006 (b), and 2007 (c). Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in inorganic nitrogen among field types and an asterisk (*) designates a significant difference ($P < 0.05$) in inorganic nitrogen between and under perennial grasses within a field type.

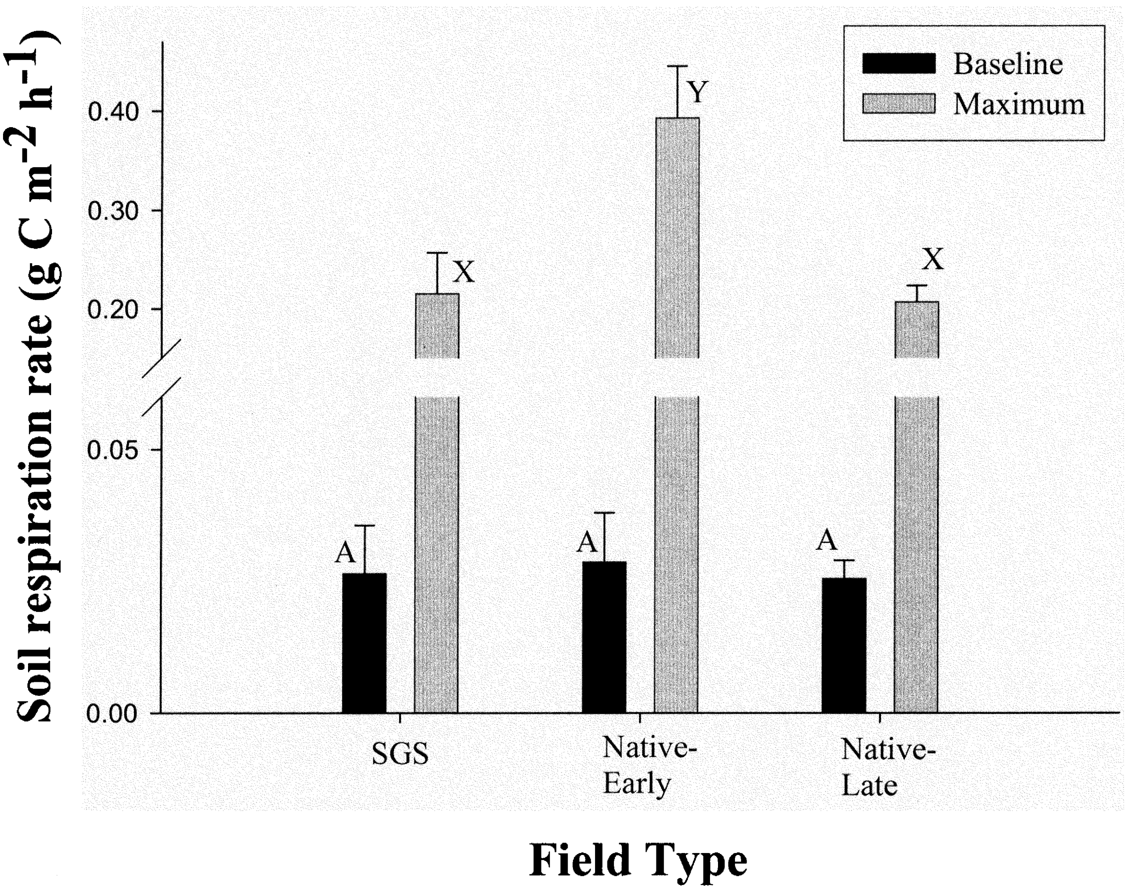

Figure 6. Baseline and maximum soil respiration rate (g C m^{-2} h^{-1}; ± SE) in undisturbed shortgrass steppe (SGS), early, and late CRP fields seeded with a native seed mix. Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in baseline or maximum respiration rate among field types.

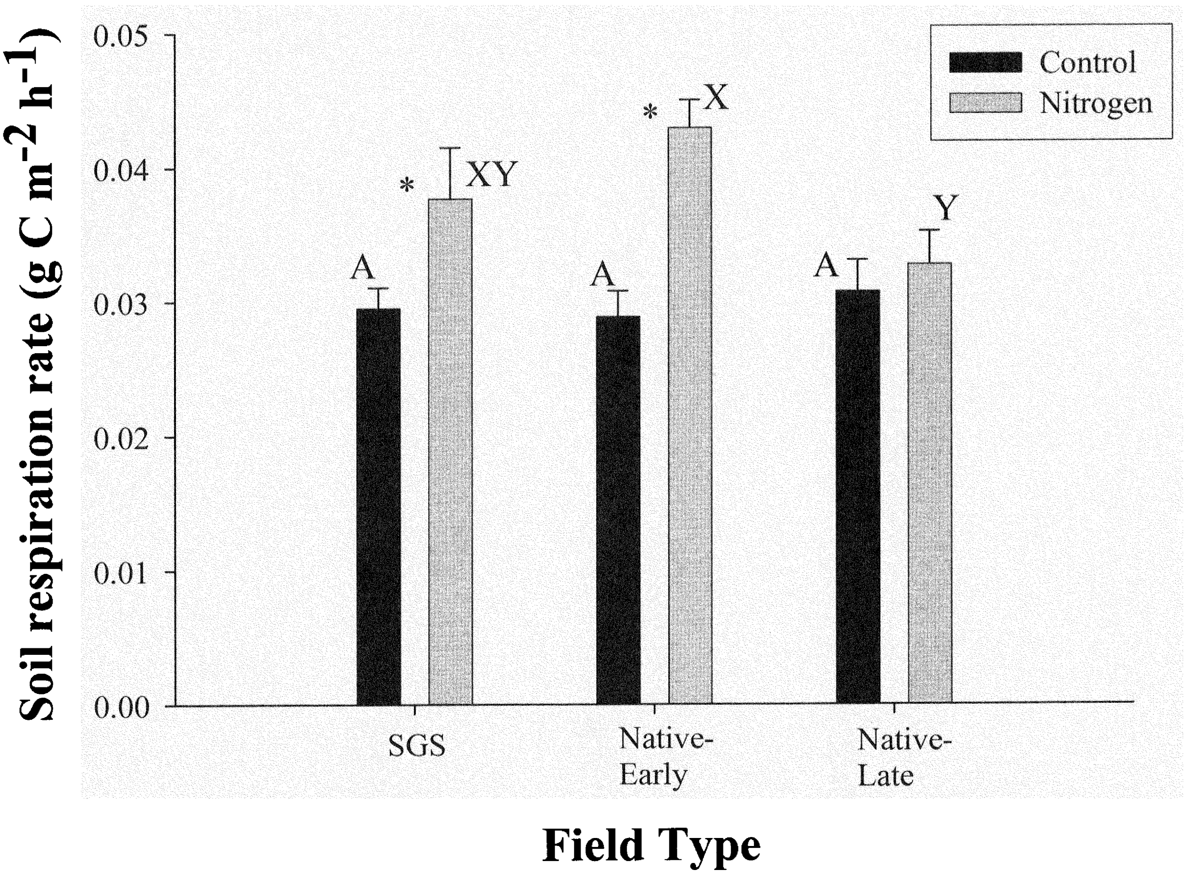

Figure 7. Soil respiration rate (g C m^{-2} h^{-1}; ± SE) in control and nitrogen addition plots in undisturbed shortgrass steppe (SGS), early, and late CRP fields seeded with a native seed mix. Different upper case letters designate significant differences (Tukey adjusted $P < 0.05$) in respiration rate among field types. An asterisk (*) designates a significant difference ($P < 0.05$) in soil respiration rate between control and nitrogen addition plots within a field type.

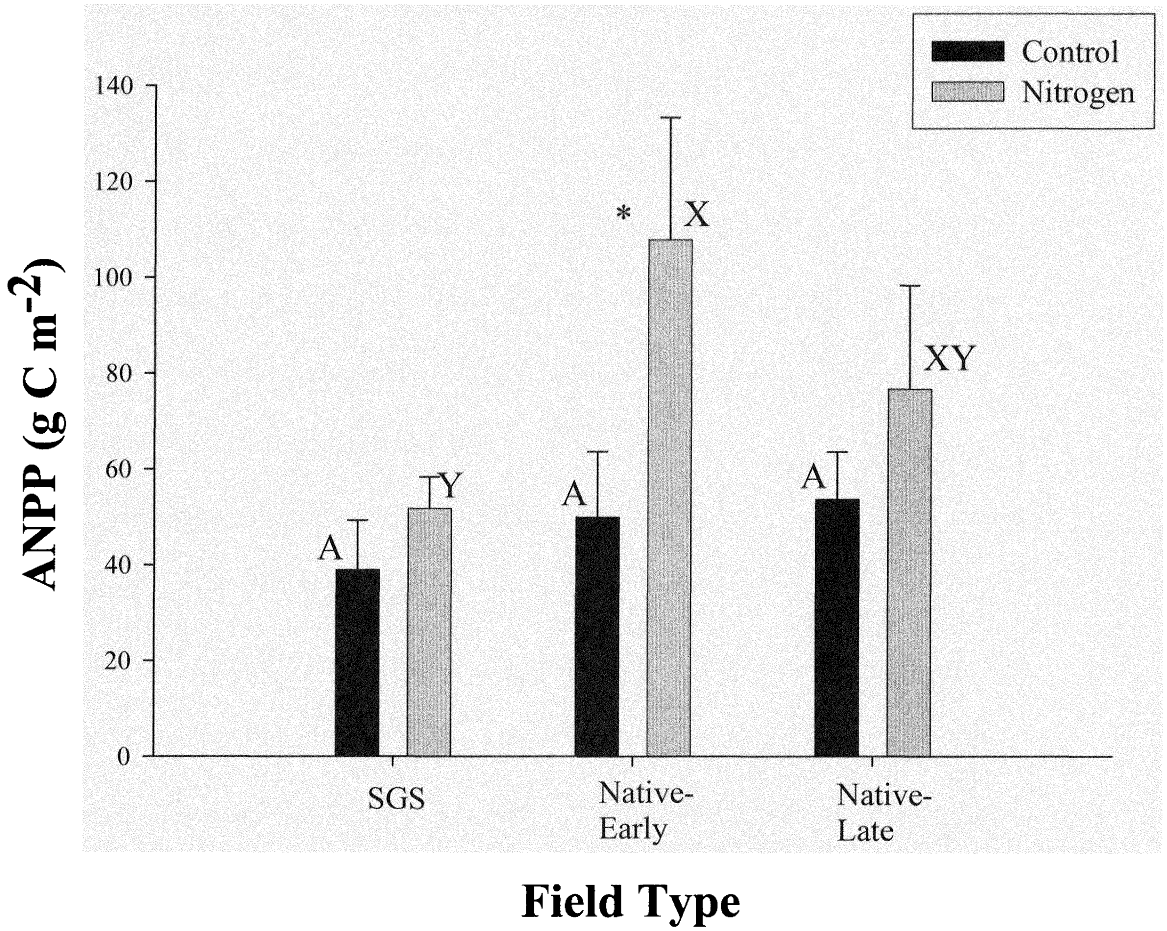

Figure 8. ANPP (g C m^{-2}; ± SE) in control and nitrogen addition plots in undisturbed shortgrass steppe (SGS), early, and late CRP fields seeded with a native seed mix. Different upper case letters designate significant differences (Tukey adjusted $P <$ 0.05) in respiration rate among field types within a treatment type. An asterisk (*) designates a significant difference ($P < 0.05$) in ANPP between control and nitrogen addition plots within a field type..

Chapter 5: Summary and Conclusions

CRP is an extensive land use (USDA Farm Service Agency 2008) that represents an important transition between wheat-fallow cropping and undisturbed shortgrass steppe in Colorado. CRP seeding practices promote the establishment of perennial grasses (Skold 1989), which provides an opportunity to study the state and rate of recovery of both plant community and ecosystem properties disrupted by cropping practices. The results from my dissertation demonstrate how time since CRP enrollment, seed mix, and environmental variability affect the following variables in CRP fields relative to the shortgrass steppe:

1. Plant community composition
2. Vegetation structure and net primary production
3. Soil carbon and nitrogen

Time since CRP enrollment explained much of the variability in plant community composition. CRP fields underwent succession as time since CRP enrollment increased. Early CRP fields had an annual forb and grass community, which was likely influenced by the seedbank and propagule pressure from nearby fields (Egler 1954). Seed mix determined which perennial grasses dominated the plant community within 18 years of CRP enrollment, but the growth of perennial grasses was slow (1% increase in canopy cover per year) compared to land converted to grasslands in more mesic regions (10-15%; Baer et al. 2002, Camill et al. 2004). This gradual recovery allowed for a dynamic plant community composed of species with different life forms, photosynthetic pathways, and origins. The amount and seasonality of precipitation affected the relative differences in canopy cover between species and functional types. Interactions among species and functional types further contributed to changes in plant community composition during succession (Connell and Slatyer 1977). High canopy cover of *Bromus tectorum*, an introduced annual grass, in mid CRP fields may have inhibited perennial grass growth. Species density declined along the chronosequence, largely driven by a loss of annual forbs, as seeded perennial grass cover increased. Species density was lowest in late CRP fields seeded with introduced perennial grasses. Native perennial grasses that were not in the seed mix colonized CRP fields; even those seeded with introduced perennial grasses, and are likely to influence future community dynamics (Coffin et al. 1996).

Vegetation structure was indirectly influenced by time since CRP enrollment and seed mix through plant community composition. The replacement of annual species with perennial grasses in CRP fields as time since CRP enrollment increased caused an increase in plant basal cover and height, and decrease in plant density. Since water availability was low, there were tradeoffs in vegetation structural characteristics. For example, tall growing introduced perennial grasses had low plant basal cover. Vegetation structure can constrain aboveground net primary production (Lauenroth and Sala 1992), but this was only apparent in CRP fields when water was not limiting. All late CRP fields had the potential to support twice as much ANPP as undisturbed shortgrass steppe in years above mean annual precipitation. In these wet years, there was a density-dependent effect on ANPP, such that each perennial grass unit in late CRP fields was more productive when it occurred at low density. Contrary to the effects introduced species may have on ANPP (Smith and Knapp 1999, Christian and Wilson 1999), there were no differences in ANPP at the field scale between fields seeded with native and introduced perennial grasses. Patterns of litter biomass in CRP fields were closely related to ANPP. In contrast to high ANPP and aboveground litter biomass, belowground biomass and belowground NPP in CRP fields was significantly lower than undisturbed shortgrass steppe, which has implications for long-term survival in a water limited region (Burke et al. 1998).

NPP inputs, respiration outputs, and soil physical characteristics determined SOC storage and were influenced by time since CRP enrollment and seed mix. No soil carbon storage occurred early in the CRP chronosequence, when NPP-C was low and potential respiration losses were high. This suggests that early CRP fields may serve as a carbon source to the atmosphere until perennial grass establishment. Perennial grasses in mid to late CRP fields increase carbon input, especially through belowground NPP-C under native perennial grasses. This supports the idea that SOC in CRP fields, like other grasslands is controlled by perennial grass root dynamics (Anderson and Coleman 1985, Dormaar 1992). SOC under perennial grasses increased by 22 g C m^{-2} y^{-1} from mid to late CRP fields and may have included the formation of recalcitrant SOC. However, carbon storage resulting from this increase was low compared to undisturbed shortgrass steppe at the field scale. Even after 18 years of recovery, late CRP fields seeded with native perennial grasses had 40% less total SOC than undisturbed shortgrass steppe. A large percentage of total SOC was associated with clay in CRP fields due to the physical and chemical stability provided by mineral organic binding (Tisdall and Oades 1982). Low BNPP-C under introduced perennial grasses led to relatively low SOC and less small scale (microsite) heterogeneity than native perennial grasses. Nitrogen (N) was closely linked to BNPP-C and SOC and recycled between vegetation and soil. N availability could largely be explained by increases in soil organic nitrogen, but was also related to belowground tissue quality and precipitation. Increases in N availability may have effects on carbon storage, especially in early CRP fields.

The research findings of this dissertation contribute to an understanding of the ecological changes that occur with shifts in land use and recovery from large scale disturbance. CRP land use facilitates a plant community dominated by perennial grasses and contributes to the recovery of ecosystem properties. Time since CRP enrollment, seed mix, and environmental variability affected plant community composition, vegetation structure and net primary production, and soil carbon and nitrogen. Within two decades of enrollment, CRP fields had a slow increase of seeded perennial grass cover, which allowed other functional types to dominate. Fields seeded with native perennial grasses were compositionally more similar to undisturbed shortgrass steppe than fields seeded with introduced perennial grasses. High above- to belowground net primary production and low vegetation basal cover in all CRP fields likely limited soil carbon and nitrogen recovery at the field scale. Low and variable water availability in this semiarid region influenced a slow, variable, and discontinuous trajectory of plant community and ecosystem recovery.

Literature Cited

Anderson, D.W. and D.C. Coleman. 1985. The dynamics of soil organic matter in grassland soils. Journal of Soil and Water Conservation 40: 211-216.

Baer, S.G., D.J. Kitchen, J.M. Blair, and C.W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications 12: 1688-1701.

Burke, I.C., W.K. Lauenroth, M.A. Vinton, P.B. Hook, R.H. Kelly, H.E. Epstein, M.R. Aguiar, M.D. Robles, M.O. Aguilera, K.L. Murphy, and R.A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42: 121-143.

Camill, P., M.J. McKone, S.T. Sturges, W.J. Severud, E. Ellis, J. Limmer, C.B. Martin, R.T. Navartil, A.J. Purdie, B.S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14: 1680-1694.

Christian, J.M. and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. Ecology 80: 2397-2407.

Coffin, D.P., W.K. Lauenroth, and I.C. Burke. 1996. Recovery of Vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications 6: 538-555.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Dormaar, J.F. 1992. Decomposition as a natural process in grasslands. Pages 121-136 *in* Coupland RT, ed. Natural grasslands: Introduction and Western Hemisphere. Elsevier, New York.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4: 412-417.

Lauenroth, W.K., and O.E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2: 397-403.

Skold, M.D. 1989. Cropland retirement policies and their effects on land use in the Great Plains. Journal of Production Agriculture 2: 197-201.

Smith, M.D. and A.K. Knapp. 1999. Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure. Oecologia 120: 605-612.

Tisdall, J.M. and J.M. Oades. 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33: 141–163.

USDA Farm Service Agency. 2008. U.S. Department of Agriculture Conservation Reserve Program acreage report summary of active and expiring CRP acres by state (as of 27 June 2008). 4 November 2008 from: http://content.fsa.usda.gov/crpstorpt/rmepegg/MEPEGGR1.HTM