

GRASSLAND RESTORATION IN A CHANGING WORLD: CONSEQUENCES OF  
RESTORATION APPROACHES AND VARIABLE ENVIRONMENTS

by

DANIEL LANPHIER CARTER

B.A., Grinnell College, 2004

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

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## Abstract

The feasibility of restoration, which traditionally targets historical conditions, is questionable in the context of global change. To address this, my dissertation investigated (Chapter 2) the patterns of restoration establishment along a chronosequence of restored prairies with respect to nearby remnant prairies, (Chapters 3-4) responses of plant communities in restorations initiated using different methods (levels of species richness and sowing density) to drought, which is projected to increase in frequency, and (Chapters 5-6) the effects of propagule source and variation (mixing among sources) on restoration establishment and the generality of restoration outcomes across variable environments using reciprocal common gardens of multi-species restoration seedings. Chapter 2, published in *Restoration Ecology*, showed that restoration led to the recovery of desirable characteristics within several years, but restorations utilizing primarily fall-collected seeds likely diminished the representation of early phenology species, so biodiversity may be further enhanced by including early phenology species in seeding mixes. Chapters 3 and 4, published respectively in *Ecological Applications* and *Applied Vegetation Science*, examined the establishment of native plant communities after seeding and their responses to experimentally imposed drought. Both high seed mixture richness and high density seeding resulted in greater establishment of native, seeded species compared to low richness and low density treatments, and exotic species were less prevalent in high richness and high density treatments. However, we found little evidence of differential drought resistance, recovery, and resilience among treatments. This result coupled with increases in exotic species following drought suggest that other forms of active management may be needed to produce restored plant communities that are robust to climate change. Chapter 5 (published in *Ecosphere*)

and Chapter 6 found that seed source affects individual species establishment, community structure, and productivity. However, there was no consistent advantage for any source, including local sources, across sites or species. This suggests that source effects on single species or effects observed at single locations should not be broadly generalized. Together, this dissertation shows that restoration can recover many characteristics of native prairies and that manipulation of seeding practices (seed mixture richness, seeding density, seed source) influence grassland establishment in terms of productivity, community structure, invasion, and the abundance and survival of individual species.

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Major Professor  
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# Table of Contents

List of Figures .....	x
List of Tables .....	xi
Acknowledgements.....	xii
Dedication.....	xiii
Chapter 1 - Introduction.....	1
Literature Cited.....	4
Chapter 2 - Recovery of Native Plant Community Characteristics on a Chronosequence of Restored Prairies Seeded into Pastures in West-Central Iowa .....	8
Abstract.....	8
Introduction.....	9
Methods .....	12
Results.....	16
Discussion.....	18
Acknowledgments .....	22
Literature Cited.....	22
Figures and Tables .....	28
Chapter 3 - High richness and dense seeding enhance grassland restoration establishment, but have little effect on drought response .....	37
Abstract.....	37
Introduction.....	38
Methods .....	42
Results.....	48
Discussion.....	51
Acknowledgements.....	56
Literature Cited.....	57
Figures and Tables .....	65
Chapter 4 - Drought-mediated stem and below-ground bud dynamics in restored grasslands ....	69
Abstract.....	69
Introduction.....	70

Methods .....	73
Results.....	78
Discussion.....	79
Acknowledgements.....	82
Literature Cited.....	83
Figures and Tables .....	90
Chapter 5 - Seed source affects establishment and survival for three grassland species sown into reciprocal common gardens.....	94
Abstract.....	94
Introduction.....	95
Methods .....	98
Results.....	100
Discussion.....	102
Literature Cited.....	105
Acknowledgments .....	105
Figures and Tables .....	110
Chapter 6 - Seed source has variable effects on community and ecosystem properties of grassland restorations sown into reciprocal common gardens .....	115
Abstract.....	115
Introduction.....	116
Methods .....	119
Results.....	122
Discussion.....	124
Acknowledgements.....	127
Literature Cited.....	127
Figures and Tables .....	133
Chapter 7 - Concluding Remarks & Recommendations.....	138
Appendix A - Chapter 1: Species Encountered and Designations.....	140
Appendix B - Chapters 2 & 3: Volumetric SWC, view of shelters, and species list.....	146
Appendix C - Chapters 4 & 5: Site characteristics, seed mixture, and additional species from chapter 5.....	158



Appendix D - Permissions from Publishers for Chapters 2, 3, & 4.....	163
Chapter 2 Permission .....	163
Chapter 3 Permission .....	167
Chapter 4 Permission .....	168

## List of Figures

Figure 2-1. Ordination plots.....	28
Figure 2-2. Boxplots for change in Simpson’s diversity, and Simpson’s evenness .....	29
Figure 2-3. Boxplots for change in native mean C .....	30
Figure 2-4. Boxplots for change in native and exotic abundance.....	31
Figure 2-5. Boxplots for mean early and late phenology richness and abundance on restorations vs. remnants .....	32
Figure 3-1. Mean species richness .....	65
Figure 3-2. Proportional resistance, recovery, and resilience.....	66
Figure 3-3. NMDS ordinations .....	67
Figure 4-1. Overall bud and stem densities .....	90
Figure 4-2. Buds per stem.....	91
Figure 4-3. Bud and stem density by functional group.....	92
Figure 5-1. Photo of <i>O. rigidum</i> seedling .....	110
Figure 5-2. Stem density and density change .....	111
Figure 5-3. Proportional survival.....	112
Figure 6-1. Conceptual framework.....	133
Figure 6-2. Biomass by species .....	134
Figure 6-3. Species richness .....	135
Figure 6-4. NMDS ordinations .....	136
Figure 6-5. Combined biomass .....	137
Figure B-1. 30 cm SWC.....	149
Figure B-2. View of shelters within experimental plots.....	150
Figure C-1. Soil texture.....	158
Figure C-2. Aboveground biomass for the species with abundance (biomass) ranks 5-8.....	159
Figure C-3. Aboveground biomass for the species with abundance (biomass) ranks 9-12.....	160

## List of Tables

Table 2-1. Restoration characteristics.....	33
Table 2-2. Spearman correlation coefficients and p-values.....	34
Table 2-3. Multiple regression output.....	35
Table 2-4. Spearman rank-order correlation by guild.....	36
Table 3-1. Significance of treatments .....	68
Table 4-1. Estimated buds per stem.....	93
Table 5-1. Statistics for Figure 2.....	113
Table 5-2. Statistics for Figure 3.....	114
Table A-1. Species Encountered and Designations .....	141
Table A-2. Cover by Species for Remnant Prairies.....	147
Table A-3. Cover by Species for Prairie Restorations.....	148
Table B-1. Species encountered.....	150
Table B-2. SAS Output Showing All Effects for Figure 3-1 .....	155
Table B-3. Least Square Means for All Treatment Main Effects in Figure 3-1 .....	157
Table C-1. Site Description.....	161
Table C-2. Species in seed additions .....	162

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## **Dedication**

I dedicate this dissertation to Thistle, who was the best thing to come of visits to my Oklahoma field site.

## Chapter 1 - Introduction

Humankind is causing an unprecedented manipulation of Earth's climate, land cover, and species distributions. Observed and projected consequences of this era dominated by human activity, informally called the "Anthropocene" (Zalasiewicz et al. 2010), are prompting societal concern and action within the management and scientific research communities. This has been especially true for temperate grasslands, where Hoekstra et al. (2005) described the disparity between habitat loss and protection as "stark". Agriculture, urban development, invasive species, and woody encroachment continue to replace or transform native temperate grassland ecosystems, and restoration has become increasingly critical for the conservation of biodiversity and ecosystem functioning (Ries et al. 2001, Baer et al. 2002, Fletcher and Koford 2003, Walker et al. 2004). However, the feasibility of restoration, which traditionally targets historical conditions (e.g. native vs. exotic species), is questionable in the context of anthropogenic alteration of biophysical conditions (Harris et al. 2006). This is the focus of my dissertation, which investigates (1) the establishment of grassland plant communities in restorations with respect to nearby remnant grasslands using a chronosequence approach, (2) responses of plant communities in restoration plots initiated using different methods (levels of seed mixture richness and sowing density) to drought, which is projected to increase in frequency over the coming decades (Strzepek et al. 2010), and (3) the effects of propagule source and variation (mixing among sources) on restoration establishment and the generality of restoration outcomes across variable environments using reciprocal common gardens in three states (NE, KS, OK), which differ markedly in their biophysical conditions.

I conducted my research in the tallgrass prairie region of central North America. Tallgrass prairie once covered over 68-million ha between Canada and Texas and Nebraska and Indiana, but most of this has been converted for agricultural purposes, and less than one-tenth of one percent of original tallgrass prairie remains in some states and provinces: Iowa, Illinois, Indiana, Manitoba, North Dakota, and Wisconsin (Samson and Knopf 1994). Remaining grasslands are economically important for grazing, provide critical habitat for flora and fauna (Allen-Diaz 1996, McKee 1998, Wolken 2001), and deliver ecosystem services, including carbon storage and enhanced water quality (Kemp and Dodds 2001, Derner et al. 2006). Biophysical changes in Central North America are ubiquitous. Invasions of exotic species (Jordan et al. 2008), changes in vegetation type (Linneman and Palmer 2006, Norris et al. 2007), increases in mean annual temperature and the frequency and intensity of summer droughts (Meehl et al. 2007, Strzepek et al. 2010), observed and continuing increases in atmospheric CO<sub>2</sub> concentrations, and N deposition all have consequences for grassland plant communities and ecosystem processes (Zaveleta et al. 2003, Stevens et al. 2004). These changes collectively place restoration science on an unsteady footing.

Restoring diverse grassland plant communities in areas where most native species have been eliminated requires seed addition, because dispersal limits the colonization of disturbed sites by most grassland species, and many grassland species do not maintain long-term seed banks (Rabinowitz and Rapp 1980). Seed mixtures, then, represent much of the available species pool (*sensu* Zobel 1997) for plant communities in grassland restoration. This underscores the importance of restoration seed mixture composition and planting methods in the context of global change, because human decisions should determine whether or not grassland restorations contain plant species or genotypes suitable for environments that are likely to deviate markedly

from historical references. In species- or functionally-rich plant communities, ecosystem functioning may be enhanced as a result of complementary patterns of resource use or greater likelihood of the presence of species that compete for resources across temporal and spatial gradients (Huston 1997; Marquard et al. 2009). Species-rich plant communities can also diminish establishment of invasive species and enhance drought resistance, recovery and resilience, if resultant communities possess greater richness and associated trait variation (Loreau et al. 2001). Trait variation associated with genetic variation within species can have similar ecological effects (Hughes et al. 2008). There are many documented examples where ecotypes of plant species (derived from different locations and assumed to be genetically distinct) exhibit differential responses to common environments (e.g. Clausen et al. 1940, Knapp and Rice 2008). Restoration seed mixture composition, then, is critical for the establishment of plant communities and their associated properties in restoration. Seed mixtures determine whether or not the traits needed to pass through abiotic and biotic filters (e.g. climate, substrate, competition, trophic interactions) for establishment and future environmental variation are present within and among species (Hobbs and Norton 2004). There are many publications on the effects of restoration practices, the structure of plant communities and ecosystem functioning in restorations, and the effects of many dimensions of global change on community and ecosystem processes. Yet there remains a scarcity of research that unites these to inform restoration in a changing world. My dissertation describes how plant communities in restorations develop, and how variable environments can act as ecological filters and interact with restoration practices that influence species pools and dispersal to affect plant community structure and productivity.



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# **Chapter 2 - Recovery of Native Plant Community Characteristics on a Chronosequence of Restored Prairies Seeded into Pastures in West-Central Iowa<sup>1</sup>**

## **Abstract**

Restored grasslands comprise an ever-increasing proportion of grasslands in North America and elsewhere. However, floristic studies of restored grasslands indicate that our ability to restore plant communities is limited. Our goal was to assess the effectiveness of restoration seeding for recovery of key plant community components on former exotic, cool-season pastures using a chronosequence of six restoration sites and three nearby remnant tallgrass prairie sites in West-Central Iowa. We assessed trends in Simpson's diversity and evenness, richness and abundance of selected native and exotic plant guilds, and mean coefficient of conservatism (mean C). Simpson's diversity and evenness and perennial invasive species abundance all declined with restoration site age. As a group, restoration sites had greater richness of native C3 species with late phenology, but lower richness and abundance of species with early phenology relative to remnant sites. Total native richness, total native abundance (cover), mean C, and abundance of late phenology C3 plants were similar between restoration and remnant sites. Observed declines in diversity and evenness with restoration age reflect increases in C4 grass abundance rather than absolute decreases in the abundance of perennial C3 species. In contrast to other studies, restoration seeding appears to have led to successful establishment of tallgrass prairie species

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that were likely to be included in seeding mixtures. While several floristic measures indicate convergence of restoration and remnant sites, biodiversity may be further enhanced by including early phenology species in seeding mixes in proportion to their abundance on remnant prairies.

## **Introduction**

Hoekstra et al. (2005) describe the disparity between habitat loss and protection in temperate grasslands as “stark” and classify temperate grasslands among the most critically endangered ecoregions globally. In North America, tallgrass prairie once covered over 68-million ha, but tallgrass prairie extent has declined dramatically since the 1800s with increased agricultural land use. One-tenth of 1% or less of original tallgrass prairie remains in Iowa, Illinois, Indiana, Manitoba, North Dakota, and Wisconsin (Samson & Knopf 1994). Work in temperate grasslands (Foster et al. 2007; Jiang et al. 2010; Kiehl et al. 2010) has demonstrated dispersal limitation in grassland establishment. In North American grasslands, dispersal and establishment may take centuries without intervention (Foster et al. 2007). The first researched attempts at grassland restoration via the introduction of seeds or transplants began in the 1930s with the J.T. Curtis prairie at the University of Wisconsin Arboretum (Cottam & Wilson 1966), and in recent decades there have been increased efforts to restore prairie for both conservation and research purposes (Mlot 1990). While remnant prairies are of critical conservation concern, small-scale restoration efforts and large projects like the Neil Smith National Wildlife Refuge, Iowa (US Fish and Wildlife), and projects undertaken by the Nature Conservancy have increased the relative importance of restored tallgrass prairies for harboring biodiversity and performing ecosystem functions. Restoration can serve as an “acid test” of our understanding of community assembly (Bradshaw 1987). While restoration of some grassland and forest systems has met with

some success (Hellstrom et al. 2009; Bruel et al. 2010; Mackenzie & Naeth 2010), reestablishing plant diversity in tallgrass prairie remains elusive (Camill et al. 2004). Kindscher and Tieszen (1998), Sluis (2002), Martin et al. (2005), McLachlan and Knispel (2005), and Middleton et al. (2010) investigated floristic patterns on ex-arable sites restored by seed addition with respect to remnant sites and found that restorations were floristically impoverished after as many as 35 years relative to remnant prairies. These authors concluded that restorations using seeds do not recover floristic patterns typical of remnant prairies, at least in the near term. A number of studies have indicated that older restorations exhibit a shift toward excessive C4 grass dominance (Baer et al. 2002; Camill et al. 2004; McLachlan & Knispel 2005) at the expense of floristic diversity. It is unclear why C4 grasses collected from local remnant prairies appeared to exclude other native species more in restorations than nearby remnant prairies, and Camill et al. (2004) speculated that this may result from altered burn regimes, pressures from primary consumers, and problems with restoration practices. Soil resource heterogeneity can also influence patterns of C4 grass dominance in restorations (Baer et al. 2005). The degree to which restored plant communities successfully exclude exotic species is unclear. In several studies, increases in native plant cover, largely C4 grasses, coincided with decreases in the cover of weeds (both native and exotic ruderal species) as restorations age (Baer et al. 2002; Camill et al. 2004; McLachlan & Knispel 2005). However, there has been little focus on trends in the abundance of exotic perennials with restoration age (but see McLachlan & Knispel 2005 for trends in exotic, cool-season grasses) despite the threats that exotic perennial species pose to the diversity and functioning of prairies in Central North America (Symstad 2004; Woods et al. 2009). Our first objective was to assess trends in several key characteristics of prairie plant communities restored by seeding in the context of former exotic, cool-season pastures. Most

other studies have assessed prairie restorations on ex-arable lands, and conclude that seeding alone is insufficient for establishing plant communities similar to remnant prairie. Restoration in the context of cool-season pastures is seldom studied, and could have consequences for patterns of ruderal and exotic abundance and the establishment of native richness and abundance that differ from those on ex-arable lands. Our second objective was to present and compare trends in several underlying plant community characteristics. Many studies of plant community dynamics across restoration chronosequences (Kindscher & Tieszen 1998; Sluis 2002, Camill et al. 2004; McLachlan & Knispel 2005) or comparisons of restored to remnant plant communities (Martin et al. 2005) do not explicitly consider differences in native species characteristics (i.e. whether restored communities consist of the same native species that tend to be found in remnant prairies), and few track guild-specific trends (Camill et al. 2004). Instead, most authors have reported changes in native plant richness and diversity or evenness. Here, we report mean coefficient of conservatism (mean C) values, defined in the Methods section, which Taft et al. (2006) indicate may better capture qualitative differences among sites by differentially weighting ruderal versus conservative components of native plant communities. We also report temporal trends in richness and abundance within selected native and exotic plant guilds, temporal trends in plant community summary variables (native diversity, evenness, and mean C), associations between community summary variables and the abundance of different plant guilds, and differences between grouped restoration and remnant sites. Analysis of subgroups highlights characteristics that might underlay broader measures (richness, evenness, etc.) and identify pitfalls in restoration for further exploration.



## **Methods**

### ***Study Sites***

Tallgrass prairie restorations were located at Diversity Farms, Inc. (41°53' N, 94°47' W), approximately 100-km west-northwest of Des Moines, IA. Remnant prairie sites were located within a 25-km radius. All locations were designated as prairie by the General Land Office survey of Iowa that occurred from 1836 to 1859. Prairie restoration sites were enrolled from row-crop agriculture into the Conservation Reserve Program (CRP) in 1986 and seeded to *Bromus inermis* (smooth brome) pasture. Beginning in 1998, Diversity Farms, Inc. applied glyphosate to portions of the original (CRP) fields and subsequently burned them to remove standing litter. Restorations were then planted by broadcast seeding over uncultivated soil using bulk, unprocessed seed harvested in the fall by combine and small amounts of seed harvested by hand from prairie remnants within a one-county radius (approximately 80-km), including the remnant prairies sampled for this study. Bulk seeding rates (including hand harvest) for forbs were double those for grasses (1.4- to 1.8-kg/ha forb; 0.7- to 0.9-kg/ha grass), and reflected seed production of species bearing seeds at bulk harvest dates in autumn. All prairie restorations were contiguous, occupied a similar upland rolling topography, and were burned in spring on an annual basis after their first burn. Restorations were also mowed as needed to reduce competition from weeds. All remnant sites were managed by Diversity Farms, Inc. with a spring fire return interval of 2 or 3 years and utilized for seed collection. Table 2-1 contains additional site and management information.

### ***Vegetation Sampling***

In both mid-May and early August, 2009, a fixed-location, modified Whittaker sampling scheme was used within each site to (1) sample both species richness and species-specific total canopy cover in ten  $0.5 \times 2$ -m subplots arrayed around a  $20 \times 50$ -m rectangle and (2) sample only species richness in two  $2 \times 5$ -m subplots, one  $5 \times 20$ -m plot, and an inclusive  $20 \times 50$ -m plot (Stohlgren et al. 1995). All modified Whittaker plots were located at least 10-m from site-edge transitions, and situated along maximum available gradients of slope. Benefits of this sampling method included the minimization of codependence among subplots, better estimates of site richness, and standardization of sampling area across sites (Stohlgren et al. 1995).

### *Vegetation Analyses*

We assessed species richness at  $1\text{-m}^2$  ( $n = 10$ ),  $10\text{-m}^2$  ( $n = 2$ ),  $100\text{-m}^2$  ( $n = 1$ ) and  $1,000\text{-m}^2$  ( $n = 1$ ) spatial scales at each site. At the 1- and  $10\text{-m}^2$  scales, we calculated richness as the mean number of species across subplots encountered on at least one of the two sampling occasions; at the 100- and  $1,000\text{-m}^2$  scales, richness was the total number of species encountered. We assessed abundance by species as peak total canopy cover attained on each subplot across sampling occasions. Unless otherwise stated, reported values reflect total percent cover. Peak total cover values could be greater than 100% because of multilayered vegetation canopies or replacement among species from May to August. We assessed abundance of both ruderal (annual and biennial) and perennial native and exotic species and patterns of richness and abundance for several native perennial guilds. These included Asteraceae, Fabaceae,  $C_4$  graminoids, and  $C_3$  graminoids, which were defined previously as functional groups with slight variations because they respectively represent the greatest richness component, nitrogen fixers, and two carbon fixation pathways among dominant perennial graminoids (Kindscher & Wells 1995, Tilman 1997, Camill et al. 2004). We also assessed early and late phenology guilds of perennial  $C_3$

species independently, because C<sub>3</sub> species with early phenologies had high abundance on studied remnants and disperse seeds prior to bulk seed collections at these sites. These phenology guilds are analogous to Kindscher and Wells' (1995) C<sub>3</sub> grasses and sedges, ephemeral spring forbs, and spring forbs combined (early phenology) and summer/fall forbs and legumes combined (late phenology). Phenology, native/exotic, and perennial/biennial/annual guild designations for species and site presence for species are given in Appendix A. Plant species nomenclature follows the United States Department of Agriculture Plants Database. We calculated mean 1-m<sup>2</sup> Simpson's diversity and evenness (Simpson 1949; Magurran 2004) using peak total cover as the measure of abundance for each species. Trends in the site presence of native species that tend to be restricted to relatively undisturbed, native prairie were assessed using the coefficient of conservatism (CC), which weights species on a scale from 1 to 10, with greater values assigned to species that tend to be restricted to relatively undisturbed remnant sites (Swink & Wilhelm 1994). Taft et al. (2006) found that CC explained more variation among tallgrass prairie sites than conventional plant community measures. We used CC values developed for Iowa, available through the Ada Hayden Herbarium at Iowa State University, and calculated the mean C weighted by species' relative abundances for each site:

$$\text{Mean C} = \sum CC_i \cdot A_i$$

where A is the relative abundance (based on peak values) for the *i*th species in each subplot. We also present the analysis used by Taft et al. (2006), which divides the sum of CC values by native richness without weighting by abundance.

## *Statistical Analyses*

We used permutational multivariate analysis of variance (MANOVA) to perform global tests of the difference among all sites at the 1-m<sup>2</sup> scale based on the 10 subplots within each site and the difference between pooled restoration (n = 6) and remnant (n = 3) sites to assure the existence of site differences when performing univariate analyses. Refer to Anderson (2001) for an introduction to permutational MANOVA. We also performed canonical variates analysis (CVA) on multivariate data to visualize the distance between and among plant communities at restoration and remnant sites in a reduced dimensional space (Johnson 1998). This analysis illustrates similarity among communities with respect to all plant guild and community summary variables. This was preferred to community similarity analyses based on the presence and abundance of individual species. We used two-sample permutation tests based on means (10,000 iterations) to assess differences in plant community structure variables between restoration sites (n = 6) and remnant sites (n = 3) where  $D_{obs}$  is the observed difference in means between restorations and remnants.

We explored changes in plant community structure with age across the restoration chronosequence using Spearman rank correlation (approximate permutation method, 10,000 iterations). We assessed relationships between the response variables Simpson's diversity, Simpson's evenness, and mean C and the predictor variables native C<sub>4</sub> abundance, native perennial C<sub>3</sub> abundance, and ruderal species abundance using linear multiple regression. Permutational tests were used in cases where assumptions of parametric tests were violated or for consistency where parametric statistics were appropriate for only a minority of tests. Spearman correlations were used to assess trends with respect to restoration age, because Spearman correlations do not assume that trends are linear. Permutation MANOVA, univariate tests, and

tests of association were performed in Program R version 2.10.1 (2009), including the coin (Hothorn et al. 2008) and vegan (Oksanen et al. 2010) packages. CVA was performed with SAS version 9.2 (2000–2008) using the PROC GLM procedure. All analyses of trends with restoration age utilized subsamples as separate observations within each restoration site. This approach is common in grassland chronosequence studies because of constraints in the replication of treatments at large spatial scales (Matamala et al. 2008).

## **Results**

### ***Multivariate Analyses***

Permutation MANOVAs indicated significant differences among individual restoration and remnant sites (pseudo-F=14.616,  $p < 0.001$ ) and between pooled restoration and remnant sites (pseudo-F=16.954,  $p < 0.001$ ). All restored plant communities significantly differed from all remnant communities, but were similar to one-another with respect to the first canonical variate (CVA), and all remnant sites differed from one-another (Figure 2-1). Restored and remnant communities also differed with respect to the second canonical variate, with the greatest differences among plant communities at restored sites (Figure 2-1). The first canonical variate was positively associated with measures of early phenology richness and abundance, and the second canonical variate was negatively associated with several variables that reflect ruderal or exotic character and positively associated with variables that represent native components of the plant community seeded into the restorations (Table 2-2).

### ***Native and Exotic Richness***

Native species richness did not differ significantly between restoration and remnant sites at any scale, and showed no significant correlation with restoration age. Exotic richness

decreased with restoration age at all scales sampled (1,000-m<sup>2</sup>,  $r_s=-0.786$ ,  $p=0.007$ ; 100-m<sup>2</sup>,  $r_s=-0.926$ ,  $p=0.015$ ; 10-m<sup>2</sup>,  $r_s=-0.747$ ,  $p=0.004$ ; 1-m<sup>2</sup>,  $r_s=-0.786$ ,  $p<0.001$ ).

### ***Simpson's Diversity and Evenness***

Both Simpson's diversity and evenness for native species declined with restoration age (Figure 2-2). Fits of linear multiple regression models containing C<sub>3</sub> and C<sub>4</sub> native, perennial abundance and native ruderal abundance as predictors were not significantly different from models with C<sub>4</sub> abundance as the sole predictor and yielded similar coefficients of determination for both indices (Table 2-3), suggesting that values for both indices across restoration sites were explained by increases in C<sub>4</sub> grass abundance rather than absolute declines in C<sub>3</sub> perennial abundance. There were no significant differences in Simpson's diversity or Simpson's evenness between grouped restoration and remnant sites, although older restoration sites had low Simpson values with respect to two of three remnant sites.

### ***Mean C***

Native mean coefficient of conservatism (mean C) weighted by relative abundance increased with restoration age, although the increase appears nonlinear, and un-weighted native mean C showed no association with restoration age (Figure 2-3). For both forms of mean C, linear multiple regression model fits containing C<sub>4</sub> and C<sub>3</sub> native, perennial abundance and native ruderal abundance as predictors were not significantly different from models with perennial C<sub>3</sub> and ruderal abundance as predictors and yielded similar coefficients of determination (Table 2-3), suggesting that perennial C<sub>3</sub> and ruderal species rather than C<sub>4</sub> grasses predict mean C.

### ***Native and Exotic Abundance***

Abundance of native species increased non-linearly with restoration age (Figure 2-4a), and exotic abundance decreased with restoration age (Figure 2-4b) and was lower in the oldest three restorations compared to the three remnant prairies (Dobs=1.569, n=m=3, p=0.045). Declines in abundance also occurred among exotic perennial species (Figure 2-4b).

### ***Abundance and Richness for Selected Native Plant Guilds***

Native C<sub>4</sub> grass abundance increased with restoration age, and both ruderal and early phenology richness and abundance decreased (Table 2-4). Early phenology richness and abundance were trivial in comparison to late phenology richness and abundance across restoration sites (Figure 2-5), so trends for early phenology species had little influence on overall richness and abundance at restoration sites. Overall, C<sub>3</sub> richness and abundance did not significantly decline with restoration age.

Both richness and abundance for early phenology C<sub>3</sub> species were greater on remnant sites than on restorations (Figure 2-5a,b). However, no differences were detected between restorations and remnants in abundance of late phenology C<sub>3</sub> species, and 1-m<sup>2</sup> late phenology C<sub>3</sub> species richness was greater in restored prairies than remnants (Figure 2-5c,d). Richness for C<sub>4</sub> species was marginally higher in restored prairies (D.obs=0.487, p=0.056).

## **Discussion**

While the thesis that restoration of tallgrass prairie from seed does not successfully establish communities similar to remnant sites (e.g. Sluis 2002; Camill et al. 2004; Middleton et al. 2010) appears to be supported by observed patterns in Simpson's diversity and evenness and multivariate analyses, restoration sites in this study developed and maintained several aspects of native plant community structure similar to nearby remnant prairies. We found no significant

differences in native species richness between restored and remnant prairies, no evidence for a negative association between native richness and restoration age at any sampling scale, and no evidence for a difference in mean C between restored and remnant prairies. The finding that 1-m<sup>2</sup> richness for late phenology perennial forbs was higher on restoration sites than remnant sites contradicts the general conclusions of many previous studies.

Simpson's measures and mean C showed conflicting trends, because Simpson's diversity and evenness were predicted by different underlying components of the plant communities than both weighted and unweighted mean C. Declines in Simpson's diversity and evenness with restoration age were not associated with declines in total C<sub>3</sub> perennial abundance, but rather an increase in C<sub>4</sub> abundance similar to that observed by Baer et al. (2002) and Camill et al. (2004). Hence, Simpson's diversity and evenness were poor metrics for C<sub>3</sub> presence on these restoration sites. Conversely, mean C showed a strong positive relationship with perennial C<sub>3</sub> abundance and negative relationship with C<sub>3</sub> ruderal abundance.

Explicit differences between the results of this study and those of Sluis (2002) and others are primarily confined to overall richness and may have multiple causes. Prolonged perennial cover, the lack of cultivation to prepare the seed bed, or differences in nutrient availability on former cool-season pastures relative to ex-arable lands may have favored native perennial over ruderal species on our restoration sites (e.g. Blumenthal et al. 2003; Rashid & Reshi 2010). Establishment of richness and abundance patterns on restorations may have also been facilitated by mowing on multiple occasions to prevent the development of closed weed canopies (Wilson & Clark 2001), or by the prescription of fire, which can have negative effects on seed viability (Vermeire & Rinella 2009) and promotes prairie vegetation (Anderson 1990). Germination for many forbs is encouraged with cold stratification (Shirley 1994), so fall seeding on most



restoration sites may have favored early forb establishment. Also, the seeding ratio of forbs to grasses was high, which has been shown experimentally to promote the establishment of forb richness (Dickson & Busby 2009).

Mean C provided insight into the process of community establishment across the chronosequence. Weighted mean C on restored prairies was positively associated with restoration age while un-weighted mean C showed no association. These mean C patterns and overall species richness patterns were consistent with initial floristics succession (*sensu* Egler 1954), where prairie species (with high mean C) established early in the restoration chronosequence and subsequently increased in abundance as richness remained relatively constant. This suggests that weighted mean C captures successional changes better than un-weighted Mean C and that high mean C species can increase in abundance after initial establishment without subsequent seeding.

The overall increase in native abundance across the chronosequence was consistent with trends reported by Baer et al. (2002) and Camill et al. (2004), and corresponded to decreases in exotic richness and abundance. Exotic perennials decreased with restoration age and were less abundant on older restorations than remnant prairies, despite initiation of restorations on ground formerly dominated by these exotic, sometimes invasive, perennials. Observed patterns of perennial exotic richness and abundance may be explained complementarity or sampling effects from an enhanced pool of species in restoration seeding mixes drawn from varied remnant sites, if species in seed mixes more completely utilized limiting resources (Fargione & Tilman 2005; Marquard et al. 2009). High fire frequency on restorations, which can have negative effects on C<sub>3</sub> species (Howe 1994; 2000), may also explain these patterns. All perennial exotic species observed possess the C<sub>3</sub> photosynthetic pathway. Native C<sub>3</sub> species in the restorations may have

responded differently, because most possess later phenology than observed exotic perennial C<sub>3</sub> species, and prescribed burns occurred early in the growing season. This is consistent with the observation that early phenology native C<sub>3</sub> species declined across the chronosequence (although initial richness and abundance of early phenology native species was low) while late phenology C<sub>3</sub> species did not.

Representation of early versus late phenology species was an important difference between restoration and remnant sites in both multivariate (CVA) and univariate analyses. Restorations were relatively poor in early phenology C<sub>3</sub> species, which agrees with qualitative observations by Kindscher and Tieszen (1998) and Martin et al. (2005). Low early phenology species richness in restorations appears to be offset by high late phenology C<sub>3</sub> species richness. Late phenology species were likely to be represented in fall bulk seed harvests, and restorations were planted with seeds from multiple remnant sites, which may explain late phenology presence and abundance patterns. For example, four blazing star species (*Liatris aspera*, *L. punctata*, *L. pycnostachya* and *L. squarrosa*) were not observed together on any one remnant site, but all were observed on restorations under similar conditions. Most early phenology C<sub>3</sub> species encountered on restorations were the focus of hand-collection efforts or retain mature seeds into the fall. The importance of these patterns should not be understated, because they suggest that observed floristic differences between restorations and remnants may not be due to an inability of sown species to establish under the management regime employed, but by underrepresentation of early phenology species in seed mixtures. Establishment of plants is often limited by dispersal in tallgrass prairie and elsewhere (eg., Tilman 1997; Foster et al. 2007; Uiarde et al. 2010), so seeding mixtures may represent the available species pool (*sensu* Zobel 1997) for many restoration projects. Reduced functional diversity resulting from underrepresentation of early

phenology species or other groups could have consequences for ecosystem functioning (Tilman 1997; Marquard et al. 2009), consumers (Symstad et al. 2000), and invasion (Fargione & Tilman 2005). Future restoration studies should explore patterns among functional groups so potential mechanisms underlying restoration outcomes may be identified for manipulation. These patterns and potential causes may not be revealed by analyses of only one or a few community indices or overall species richness. Our study suggests that manipulation of early phenology species abundances in tallgrass prairie restorations and manipulation of conditions that influence early phenology species establishment would be informative.

### ***Implications for Practice***

- Seed from remnant grasslands may be used to establish prairie vegetation on former cool-season pastures.
- Increased representation of early phenology species in seed mixes should be explored as a way of enhancing biodiversity on tallgrass prairie restorations.
- Vegetation monitoring programs concerned with the establishment of biodiversity on restorations should consider the use of weighted mean C.

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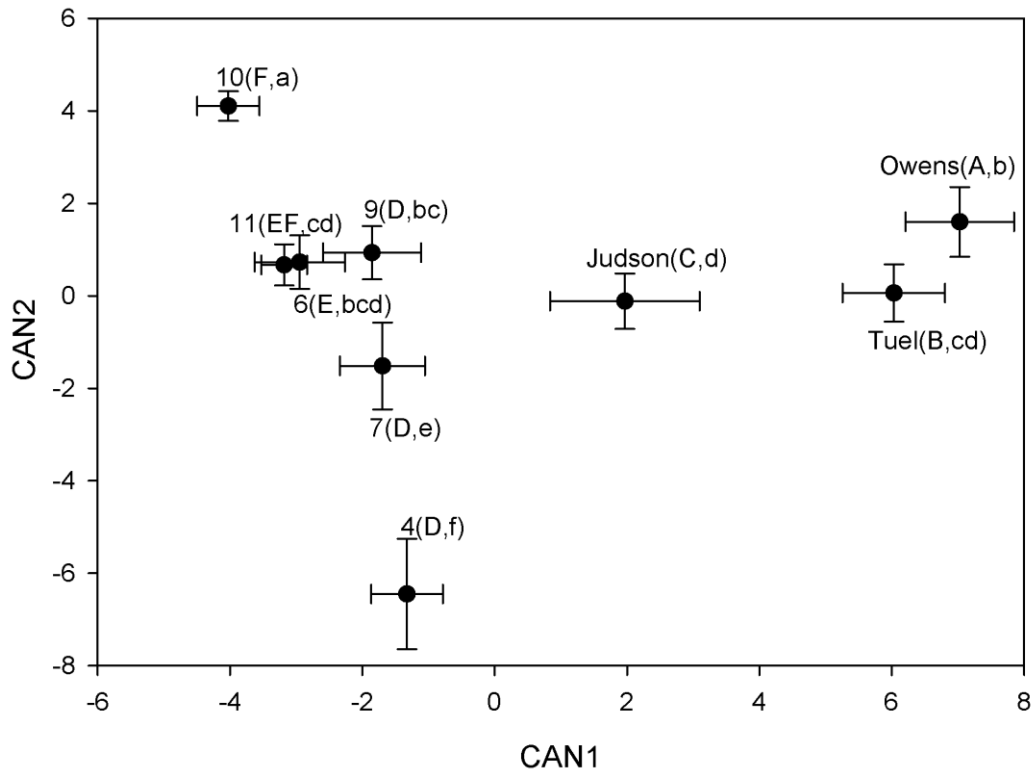
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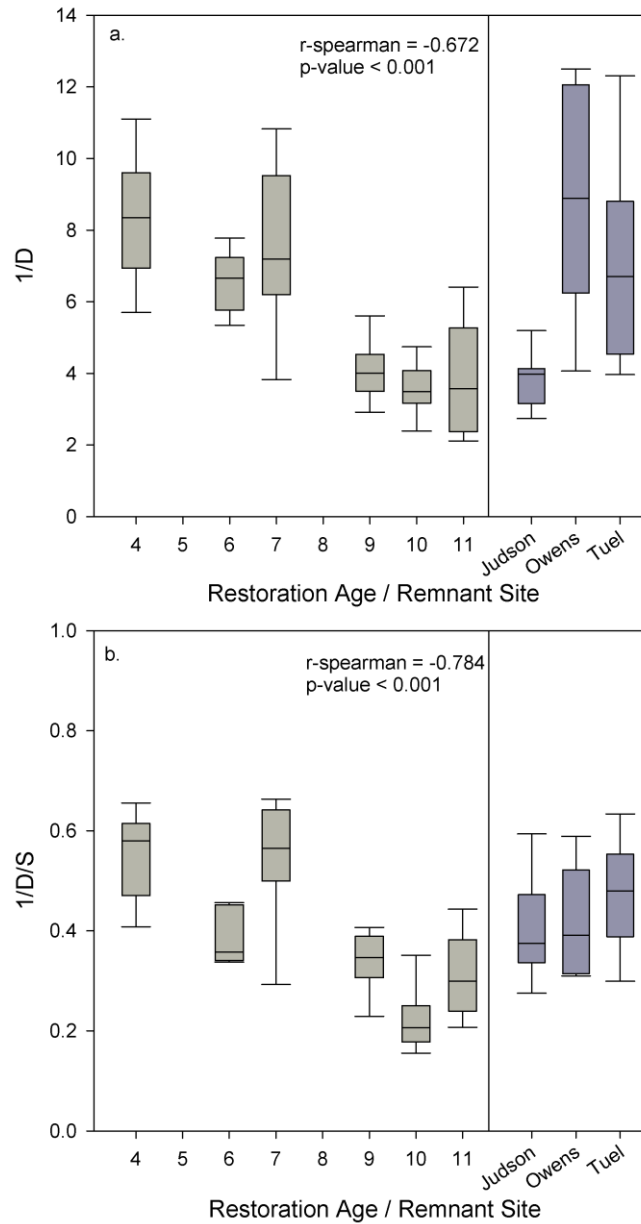
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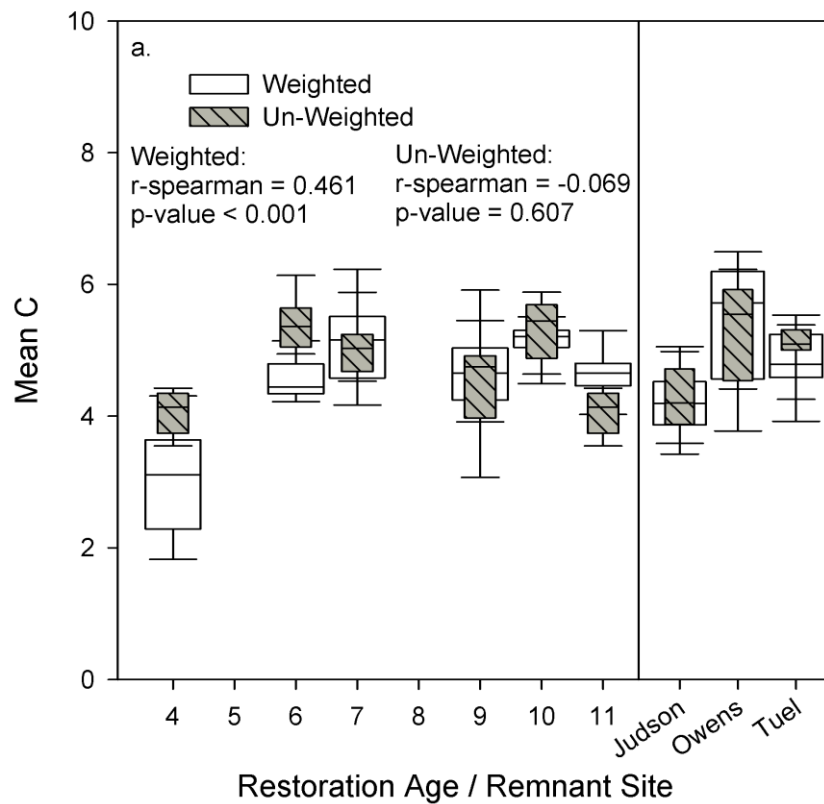
## Figures and Tables



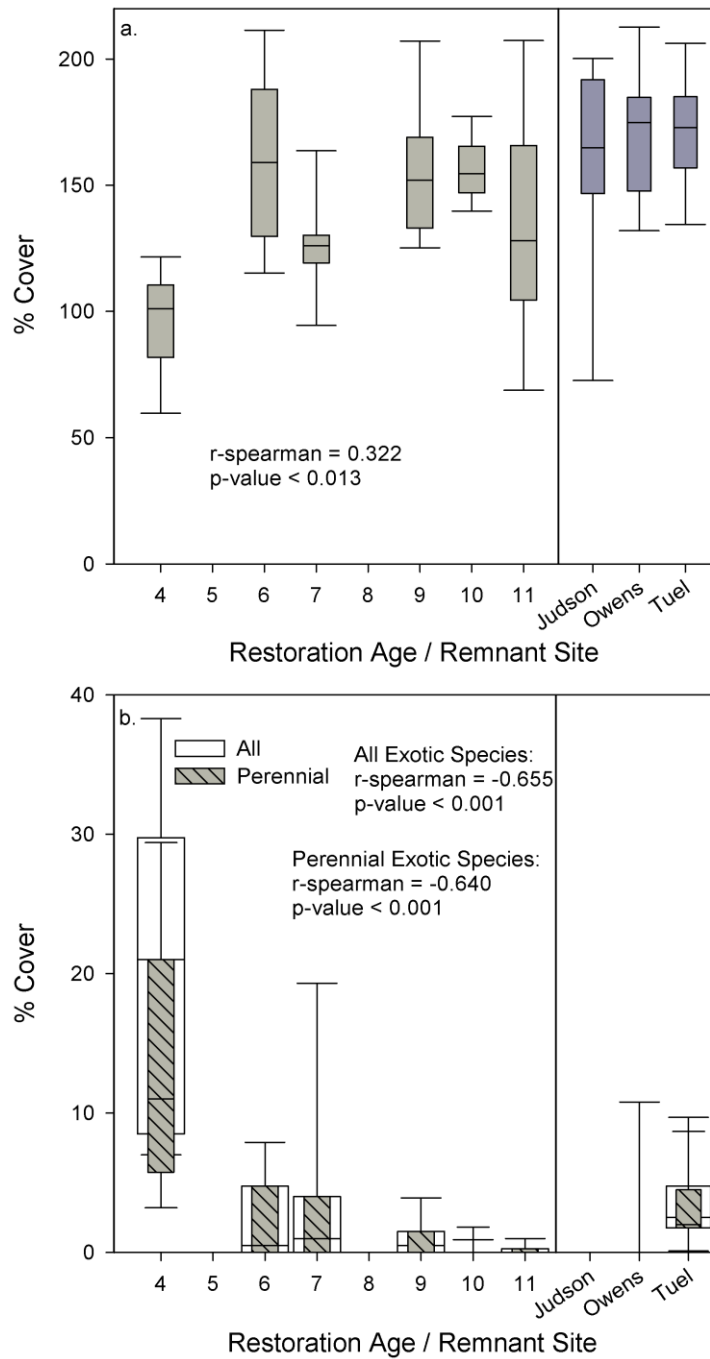
**Figure 2-1.** Ordination of means for first two canonical variates with 95% confidence intervals for six restoration (denoted by age) and three remnants sites (denoted by site name). Correlation between CAN1 and CAN2 did not significantly differ from zero, and CAN1 and CAN2 account for 67.43% of the variation among sites. ANOVA F-statistic and p-values for differences among sites: CAN1 ( $F=165.8$ ,  $p<0.0001$ ), CAN2 ( $F=81.48$ ,  $p<0.0001$ ). Letters indicate significant ( $p\leq 0.05$ ) pair-wise differences (Fischer) where significant CAN1 and CAN2 scores are represented by upper- and lower-case letters respectively.



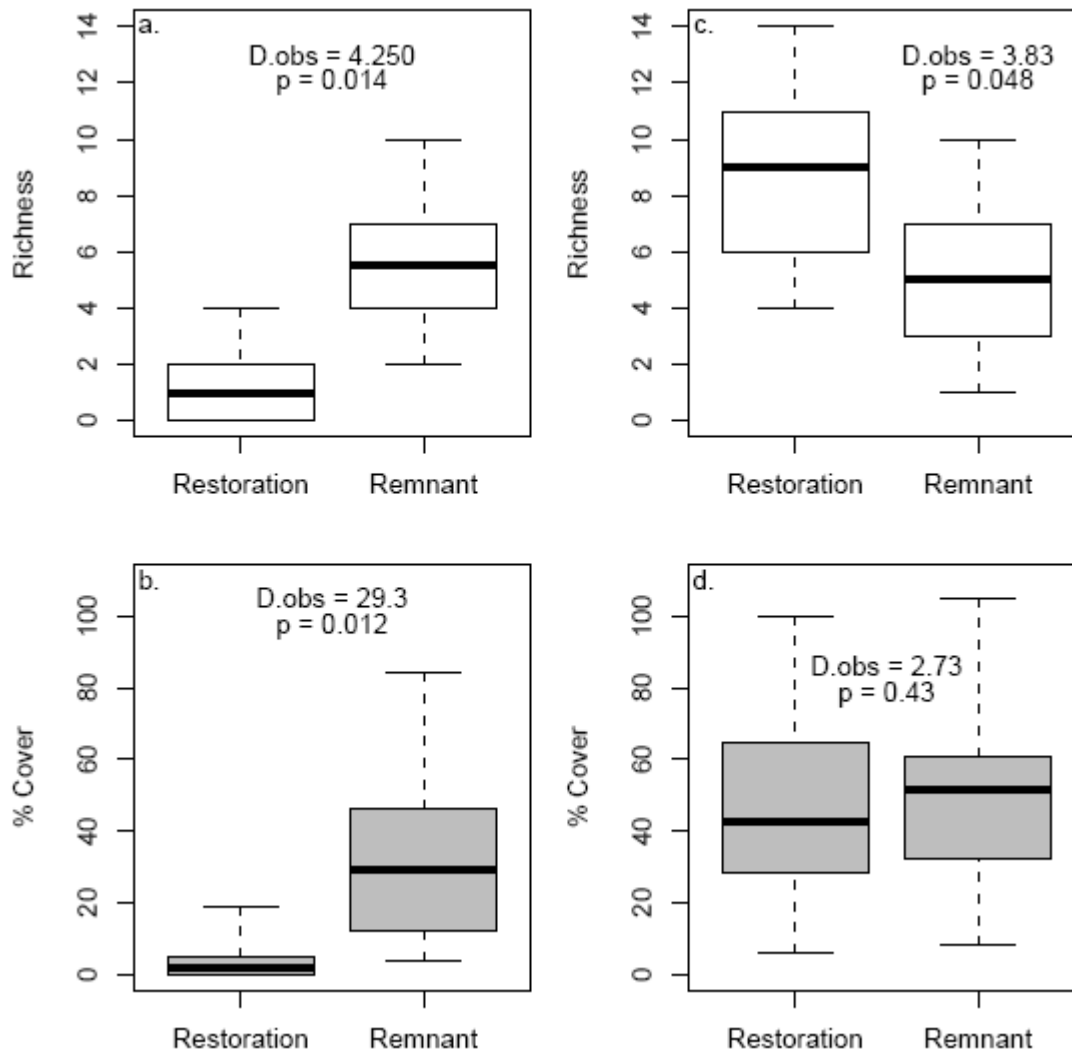
**Figure 2-2.** Boxplots for change in a) Simpson’s diversity ( $D = \text{Simpson's } D$ ) and b) Simpson’s evenness ( $S = \text{richness}$ ) with restoration age with Spearman rank correlation coefficients  $r_{\text{spearman}}$  and associated permutation p-values based on  $n=10$  subsamples for each restoration age. Simpson’s diversity and evenness values for the three remnant prairies are given for reference.



**Figure 2-3.** Boxplots for change in a) native mean C weighted by proportional abundance (white boxes) and un-weighted native mean C (grey, patterned boxes) with restoration age and Spearman rank correlation coefficients  $r_{\text{spearman}}$  and associated permutation p-values based on  $n=10$  subsamples for each restoration age. Values for three remnant prairies are given for reference.



**Figure 2-4.** Boxplots for a) change native abundance (% cover) with restoration age. b) Change in both total exotic abundance and exotic perennial abundance with restoration age. Spearman rank correlation coefficients  $r_{\text{spearman}}$  and associated permutation p-values based on  $n=10$  subsamples for each restoration age. Values for three remnant prairies are given for reference.



**Figure 2-5.** Boxplots for a) mean early phenology richness (1-m<sup>2</sup>) on restorations vs. remnants, b) mean early phenology abundance on restorations vs. remnants, c) mean late phenology species richness (1-m<sup>2</sup>) on restorations vs. remnants, and d) mean late phenology species abundance restorations vs. remnants. All comparisons are given with observed mean difference (D.obs) and permutation p-values for n=6 restorations and n=3 remnants.

**Table 2-1.** Restorations: age (number of growing seasons) and size (nearest whole hectare), time of seeding, year of first burn, number of growing seasons mowed at least one time (to approximately 20-cm with a sickle mower) after initial planting, and soil series of sampled areas; remnants: name and size (nearest whole hectare), history prior to Diversity Farms, Inc. acquisition or management (>10 years prior to study) (pasture = possibility of intermittent grazing, prairie hay = cut annually for hay, set aside = set aside for conservation by landowners at time of European settlement without history of intensive use), whether remnant had been burned since the growing season prior to sampling, and soil series.

Age (Area ha)	Year Seeded	Month	Year of First Burn	Years Mowed	Soil Series
11 (7)	1998	July	2000	3	Burchard-Adair clay loam / Ida silt loam
10 (3)	1999	November-January	2000	3	Marshall silty clay loam
9 (7)	2000	November-January	2002	3	Ida silt loam
7 (8)	2002	November-January	2004	3	Burchard-Adair clay loam
6 (6)	2003	November-January	2005	3	Ida silt loam / Marshall silty clay loam
4 (3)	2005	November-January	2007	4	Marshall silty clay loam
Remnants	History		Burned		
Judson (7)	Pasture	—	No	—	Hesch sandy loam
Owens (2)	Set aside	—	Yes	—	Sharpsburg silty clay loam
Tuel (5)	Prairie hay	—	No	—	Clarion loam

**Table 2-2.** Spearman correlation coefficients and p-values for all significant correlations ( $p < 0.05$ ) between CAN1 and CAN2 and variables used in canonical variates analysis (20 of 24 variables) in descending order of absolute value. The remaining variables (native richness,  $C_4$  richness, late phenology abundance, and *Asteraceae* abundance) were not significantly correlated with either canonical variate.

Variable	CAN1 Corr.	p-value	Variable	CAN2 Corr.	p-value
Early Phenology Richness	0.831	<0.0001	Simpson's Evenness	-0.718	<0.0001
$C_3$ Graminoid Abundance	0.806	<0.0001	Exotic Abundance	-0.523	<0.0001
Early Phenology Abund.	0.802	<0.0001	Mean C (un-weighted)	0.517	<0.0001
Other Forb Abundance	0.629	<0.0001	Perennial Exotic Abund.	-0.504	<0.0001
Late Phenology Richness	-0.577	<0.0001	Native Cover	0.503	<0.0001
<i>Asteraceae</i> Richness	-0.505	<0.0001	$C_4$ Cover	0.493	<0.0001
$C_4$ Abundance	-0.472	<0.0001	Ruderal Richness	-0.487	<0.0001
$C_3$ Abundance	0.426	<0.0001	Mean C (weighted)	0.465	<0.0001
Simpson's Evenness	0.439	<0.0001	Ruderal Abundance	-0.450	<0.0001
Simpson's Diversity	0.401	<0.0001	Simpson's Diversity	-0.432	<0.0001
<i>Fabaceae</i> Richness	-0.223	0.0326	<i>Fabaceae</i> Abundance	0.323	0.0019
.	.	.	Late Phenology Abund.	0.282	0.0071
.	.	.	$C_3$ Richness	0.257	0.0145
.	.	.	<i>Fabaceae</i> Richness	0.241	0.0222
.	.	.	Other Forb Abundance	-0.238	0.0241

**Table 2-3.** Multiple regression output for Simpson’s diversity ( $D = \text{Simpson's } D$ ), Simpson’s evenness ( $S = \text{richness}$ ), and mean C (weighted by proportional abundance and un-weighted) on restoration sites. Model specifies predictor variable(s) used:  $C_4 = \text{native perennial } C_4 \text{ cover}$ ,  $C_3 = \text{native perennial } C_3 \text{ cover}$ ,  $\text{rud} = \text{native ruderal cover}$ . ANOVA tests  $H_0$  that model fits for specified models are equal to the model:  $C_4 + C_3 + \text{rud}$ .

Response Variable	Model	p-Value	Adj. $R^2$	F-Statistic	p-Value
1/D	1: $C_4 + C_3 + \text{rud}$	<0.001	0.484	...	...
	2: $C_4 + C_3$	<0.001	0.481	1.360	0.249
	3: $C_4$	<0.001	0.456	2.485	0.092
1/D/S	1: $C_4 + C_3 + \text{rud}$	<0.001	0.551	...	...
	2: $C_4 + C_3$	<0.001	0.559	<0.001	0.993
	3: $C_4$	<0.001	0.564	0.159	0.853
Mean C (weighted)	1: $C_4 + C_3 + \text{rud}$	<0.001	0.484	...	...
	2: $C_3 + \text{rud}$	<0.001	0.480	1.402	0.240
	3: $C_3$	0.004	0.120	21.434	<0.001
Mean C (un-weighted)	1: $C_4 + C_3 + \text{rud}$	<0.001	0.267	...	...
	2: $C_3 + \text{rud}$	<0.001	0.278	0.148	0.702
	3: $C_3$	<0.001	0.181	4.859	0.017



**Table 2-4.** Spearman rank-order correlation between site age and both abundance (% cover) and richness by guild. Correlation is restricted to native species. All guilds, with the exception of ‘ruderal’, include only perennial species. Significant p-values ( $\alpha \leq 0.05$ ) are in bold.

Guild	Abundance		Richness	
	$r_{\text{spearman}}$	p-value	$r_{\text{spearman}}$	p-value
C <sub>4</sub>	0.612	< <b>0.001</b>	0.195	0.138
C <sub>3</sub>	- 0.052	0.657	- 0.211	0.103
<i>Asteraceae</i>	- 0.139	0.296	- 0.110	0.395
<i>Fabaceae</i>	0.109	0.395	- 0.049	0.707
Early phenology	- 0.344	<b>0.008</b>	- 0.444	< <b>0.001</b>
Late Phenology	- 0.020	0.868	0.093	0.487
Ruderal	- 0.349	<b>0.004</b>	- 0.357	<b>0.006</b>

## **Chapter 3 - High richness and dense seeding enhance grassland restoration establishment, but have little effect on drought response<sup>2</sup>**

### **Abstract**

Restorations commonly utilize seed addition to formerly arable lands where the development of native plant communities is severely dispersal limited. However, variation in seed addition practices may profoundly affect restoration outcomes. Theory and observations predict that species-rich seed mixtures and seeding at high densities should enhance native plant community establishment, minimize exotic species cover, and may promote resistance and resilience to, and recovery from, environmental perturbations. We studied the post-seeding establishment of native plant communities in large grassland restoration plots, which were sown at two densities crossed with two levels of species richness, on formerly arable land in Nebraska, USA, and their responses to drought. To evaluate drought resistance, recovery, and resilience of restored plant communities, we erected rainfall manipulation structures and tracked the response of seeded species cover and total plant biomass during experimental drought relative to controls and in the post-drought growing season. High seed richness and high-density seeding treatments resulted in greater richness and cover of native, seeded species per 0.5 m<sup>2</sup> compared to low-richness and low-density treatments. Cover differences in response to seed mixture richness were driven by native forbs. Richness and cover of exotic species were lowest in high-richness and high-density treatments. We found little evidence of differential drought resistance, recovery, and resilience among seeding treatments. Increases in exotic species across years were restricted to drought

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<sup>2</sup> Reprinted with permission from the Ecological Society of America: “High richness and dense seeding enhance grassland restoration establishment, but have little effect on drought response” by D.L. Carter & J.M. Blair, 2012. *Ecological Applications*, 22, 1308-1319. Data behind all figures may be found in *Ecological Archives*: <http://esapubs.org/archive/appl/A022/068/>

subplots, and were not affected by seeding treatments. Grassland restoration was generally enhanced and exotic cover reduced both by the use of high-richness seed mixtures and high-density seeding. Given the lack of restoration treatment effects on the resistance, recovery, or resilience of seeded species exposed to drought, and the increases in exotic species following drought, other forms of active management may be needed to produce restored plant communities that are robust to climate change.

## **Introduction**

As agriculture, urban development, invasive species, and woody encroachment continue to replace or transform native ecosystems, restoration has become increasingly critical for conserving biodiversity and maintaining ecosystem functioning. Restored grasslands can support native flora and fauna, suppress exotic species at local scales, and enhance the population viability of at-risk species at larger scales when they enhance connectivity within fragmented landscapes (Ries et al. 2001, Baer et al. 2002, Fletcher and Koford 2003, Walker et al. 2004, McIntire et al. 2007, Matamala et al. 2008, Carter and Blair 2011). This may be especially critical for temperate grasslands, where Hoekstra et al. (2005) described the disparity between habitat loss and protection as “stark.” Climate change will also affect temperate grasslands, as mid-continental regions are predicted to experience increased drought risk by the late 21<sup>st</sup> century (Meehl et al. 2007). While the grassland region of Central North America has experienced drought regularly over the past millennium on both annual and decadal time scales (Stambaugh et al. 2011), the frequency of extreme drought events is expected to increase substantially in coming decades (Strzepek et al. 2010). Given drought’s historical importance, projected increases in drought frequency, and the increasing area of restored grasslands relative to native grasslands, research on the effects of drought on restored grasslands warrants priority.

Restoring diverse grassland plant communities in areas where most native species were eliminated usually requires seed additions, because dispersal limits colonization and many grassland species do not maintain long-term seed banks, even in remnant grasslands (Rabinowitz and Rapp 1980, Pywell et al. 2002, Donath et al. 2007, Foster et al. 2007). The cost of seed available for restoration is often thousands of U.S. dollars per hectare and varies among species (Kline 1997, Dickson and Busby 2009). Propagule limitation and costs underscore the importance of decisions concerning seed mixture richness and seeding methods for restoration. In species or functionally rich plant communities, ecosystem functioning may be enhanced as a result of complementary patterns of resource use or greater likelihood of the presence of species that compete for resources across temporal and spatial gradients (Huston 1997, Fornara and Tilman 2009, Marquard et al. 2009). In an analysis of the responses of 147 grassland species across 17 biodiversity experiments, Isbell et al. (2011) found that 84% of species examined contributed to ecosystem functioning at least once across years, locations, and different environmental conditions. Species-rich restoration seed mixtures may also yield plant communities that diminish establishment of invasive species and enhance drought resistance, recovery, and resilience, if resultant communities possess greater richness and associated trait variation (Loreau et al. 2001). However, the relationship between richness and invasibility, or response to drought and other disturbances, is equivocal. In separate experiments, Fargione and Tilman (2005) and Biondini (2007) reported richness-mediated suppression of invasion. Richness has also been reported to stabilize the productivity of grassland experimental plots over time and in response to drought (e.g., Tilman 1996, Allan et al. 2011). In contrast, other studies report positive associations between richness and invisibility and negative associations between richness and stability in response to drought (e.g., Stohlgren et al. 1999, Kennedy et al. 2003).

This contradiction may be an artifact of spatial scale, because at larger scales disturbance is not controlled for and may co-vary with invasion (Loreau et al. 2001). Also, Lloret et al. (2007) showed that the relationship between diversity and stability of Catalanian forests varied along an aridity gradient where relatively moist locations supported both higher tree species richness and higher proportions of drought-sensitive species, leading to diminished resistance.

Complementary patterns of resource use or greater aboveground productivity may increase stress and mortality in response to drought, leading to negative diversity–resistance relationships (Van Peer et al. 2004, Wang et al. 2007, Zavalloni et al. 2008), but these do not preclude positive associations between diversity and recovery (Wang et al. 2007). Kreyling et al. (2011) showed that extreme events can also interact with site history to influence successional dynamics, such that the determinism of community assembly does not increase along a diversity gradient. Within the constraints and caveats raised by the above studies and others, richness generally is expected to enhance resistance to invasion at the local scale, but the effects of drought on plant communities, particularly successional communities like those in restorations, are less clear.

Initial planting density can also affect establishment of native vs. exotic vegetation in restoration. With low seeding density, exotic and weedy species are more likely to arrive first at small scales through emergence from seed banks or dispersal from adjacent sites. Once established, weeds strongly suppress the establishment of target native species (Blumenthal et al. 2003). With high seeding density, the emergence of desired species will more likely be antecedent or concurrent with weeds, mitigating the negative competitive effects of weedy species in young restorations. Dickson and Busby (2009) showed that high seeding densities enhance the establishment of some species over others in a grassland restoration experiment. In species mixtures seeded at high densities, seeds of more species are expected to be applied at

small spatial scales, even when seed mixture richness is held constant. For this reason, relatively high seeding densities and seed mixture richness may have similar effects.

We utilized large grassland restoration experimental plots initiated by The Nature Conservancy (TNC) in early 2006 with a factorial combination of two levels of seed mixture richness (high richness, HR; low richness, LR) and seeding density (high density, HD; low density, LD) to explore the effects of restoration seeding methods on the establishment of grassland plant communities, and on grassland drought resistance and resilience to and recovery from (defined in Methods) an intense, simulated drought applied over the course of one growing season. Most studies to date have focused on responses to natural or simulated drought in native or semi-natural grasslands rather than restored grasslands (e.g., Frank and McNaughton 1991, Kennedy et al. 2003, Kahmen et al. 2005, Gilgen and Buchmann 2009) or have assessed responses to natural drought in synthetic communities in the absence of concurrent (spatial) non-drought controls, which assumes a pre-drought equilibrium condition against which the drought can be compared (e.g., Tilman 1996, van Ruijven and Berendse 2010). The latter are the most analogous to plant communities restored to formerly arable lands, but richness or diversity effects observed in these experiments, where community composition after planting was tightly controlled or plot/mesocosm sizes were small (but see Wang et al. 2007), may not be large enough to be apparent or substantial in relation to other sources of variation in restoration settings that occur over larger spatial scales and experience less human intervention.

We addressed several questions: (1) Do HR or HD treatments enhance grassland establishment by yielding plant communities with greater richness and cover of seeded species, lower cover of exotic species, and greater aboveground net primary productivity (ANPP)? (2) Do HR or HD treatments enhance seeded communities' drought resistance, recovery, and resilience

relative to LR or LD treatments? (3) Does community structure for native, seeded species or non-seeded species differ among seed mixture richness or seeding density treatments or shift in response to drought? (Non-seeded species are species that were not part of the restoration seed mixture.) Changes in community structure for seeded species where overall cover remains constant would indicate that differential responses of component species confer stability (e.g., Tilman 1996, Wang et al. 2007, Allan et al. 2011). Shifts within non-seeded species communities caused by seeding richness treatments independent of density would indicate that biotic interactions involving sown species are important for structuring communities of non-seeded species. (4) Are effects of seeding richness and density on establishment, resistance, recovery, and resilience additive? If seeding treatments are additive, then restoration projects may achieve similar properties using a range of seeding practices. However, higher density could diminish stability to drought differentially between high- and low-richness plots, if productivity is associated with greater drought stress or mortality and covaries with richness (Van Peer et al. 2004, Zavalloni et al. 2008). Effects of richness (realized through either HR or HD treatments) on the establishment of native grasslands and their resistance/resilience to and recovery from drought would suggest that the diversity effects detected in more controlled synthetic experiments are relevant to restored grasslands and that modulating seeding methods may facilitate restoration despite contemporary climate variability and projected climate change.

## Methods

The grassland restoration experiment was initiated by TNC in South-Central Nebraska, USA (40°41' N, 98°35' W). The experiment covers 34.4 ha in the Platte River Valley formerly utilized for intensive *Zea mays* (L.) production. Soils are generally loamy sands over deeper coarse sands (Bolent-Calamus complex, Caruso loam, Gothenburg loam, Wann loam). The

climate is continental with a mean annual temperature of 10.48°C and mean annual precipitation of 629 mm (both 1971–2000 means), 65% of which falls between 1 May and 30 August; precipitation totals (nearest station, ~15 km) for 2009 and 2010 were near average (615 and 683 mm, respectively, United States Historical Climate Network [[http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn\\_map\\_interface.html](http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn_map_interface.html)]; National Weather Service [<http://www.crh.noaa.gov/gid/>]).

### ***Seeding Experiment and Rainfall Manipulation***

The experiment consisted of 24 square whole plots (0.3 ha each), to which a factorial combination of two levels of seed mixture richness (high richness [HR] = 95 species, low richness [LR] = 15 species) and two levels of seeding density were applied, for six replicates of each richness by density combination. Treatment combinations were applied systematically rather than randomly within the plot area to facilitate seeding with a mechanical drop seeder that required calibration for changes in seeding density and to minimize changes between different mixtures. For this reason, plot row and column were modeled as random effects, but they generally provided little or no improvement for model fits (lower AIC). Equal masses of bulk seed were sown by TNC in HR and LR plots, but HR plots had slightly higher seeding densities of pure live seed than LR plots, because seed test results were not complete until after sowing (low density [LD] = 164 or 172 live seeds/m<sup>2</sup> and high density [HD] = 328 or 344 live seeds/m<sup>2</sup> for LR and HR, respectively). The magnitude of observed seed mixture richness effects far exceeded the small differences in sowing density. The Nature Conservancy collected all seeds within the Central Nebraska Platte River region and broadcast seeded over damp soils and melting snow using the drop seeder in late March and early April 2006. Proportional representation varied among taxa within treatment mixtures, with grass seeds applied at higher densities than forb seeds (~8:1).



From mid-March through early October 2009, we simulated severe drought with passive rainfall manipulation structures erected at random locations within each seeding treatment plot (24 total shelters). The shelter roofs had a distribution of clear plastic slats that intercepted ~80% of ambient rainfall using a slight modification of the design proposed by Yahdjian and Sala (2002), whose 80% interception shelters permitted > 90% transmittance of the visible spectrum (although UV transmittance was reduced), reduced soil volumetric water contents at distances 0.2 m inside from the outer edge of the shelters, but led to slightly cooler air and soil temperatures under the shelters relative to outside. We observed a 30–60% reduction in volumetric soil water content (SWC, 30 cm depth, time domain reflectometry methods) under the central 1 m<sup>2</sup> of a shelter relative to SWC measured 1.5 m outside the same shelter edges over the course of a 26-day measurement period using CS616 soil moisture probes and CR103 data loggers from Campbell Scientific (Logan, Utah, USA) (Appendix B). Reduction in SWC at 30 cm over this period provides confidence that shelters created a satisfactory drought treatment. Shelter roofing material allowed > 90% transmittance of visible light (measured using portable spectrophotometer, Analytical Spectral Devices, Boulder, Colorado, USA), consistent with Yahdjian and Sala (2002).

Each shelter consisted of clear Lexan shingles (Saudi Basic Industries, Riyadh, Saudi Arabia) bent into V shapes to divert rainfall into a gutter. Shingles were secured to a tubular metal frame with spacing for 80% coverage of a 2.5 m × 2.34 m area (not square due to a 15° tilting of the roof to divert water). These dimensions for the covered shelters were greater than those used by Yahdjian and Sala (2002). The shelters were 1.5 m tall on their high side to minimize the growth of tall vegetation through spaces between the shingles. We positioned subplots (1 m<sup>2</sup>) for sampling under the center of each shelter, paired with control (non-sheltered)

subplots located randomly either 1.5 m north or south of each shelter within each whole plot. At the cessation of drought in October 2009, we removed shelter roofs and gutter systems, but continued to use the same subplots for sampling during the subsequent recovery growing season.

### ***Vegetation Sampling and Analysis***

In both May and August 2009 and 2010, richness and canopy cover for both seeded and non-seeded species (combination of native, non-seeded, and exotic species) were estimated using a modified Daubenmire scale (1 equals present but  $\leq 1\%$ ; 2 is 2–5%; 3 is 6–25%; 4 is 26–50%; 5 is 51–75%; 6 is 76–95%; 7 is  $\geq 96\%$ ), within two 0.25-m<sup>2</sup> quadrats arrayed diagonally within each 1-m<sup>2</sup> sampling area (0.5 m<sup>2</sup> within each subplot, 1 m<sup>2</sup> total within each whole plot). Canopy cover for each species on each sampling occasion was determined using the midpoint of Daubenmire scale values and then averaging across quadrats within subplots. Peak cover for species across May and August sampling dates was used in statistical analysis to account for species with both early and late phenologies. We lumped cover estimates from three species in genus *Elymus* (L.) that were included in restoration mixtures and several exotic species from genus *Setaria* (L.), because at least two of the *Elymus* species hybridize (Nelson and Tyrl 1978) and we could not reliably separate small individuals of these genera by species in the field. Unless otherwise noted, “seeded species” for seeding mixture richness treatments refers to species seeded within treatments rather than species seeded within the experiment as a whole. Sampling was spatially constrained by the size of the shelters within each plot, so sampling provides estimates of small-scale richness rather than estimates of richness for entire seeding treatment whole plots. We wish to emphasize that, although our sampling necessarily was limited to a small area within each seeding treatment whole plot, our samples were taken from the interiors (tens of meters from plot edges) of large plots and should be relatively independent

of the responses of other seeding treatments and surrounding environments, unlike many experimental studies that manipulated species richness on the order of 1 m<sup>2</sup> in exchange for greater control over species composition (e.g., Tilman 1996, van Ruijven and Berendse 2010). We assessed patterns of cover within sown species groups for C<sub>3</sub> grass and sedge (C<sub>3</sub> graminoid), C<sub>4</sub> grass and forb species, which have been defined as functional groups (sometimes “guilds”) elsewhere (Kindscher and Wells 1995, Tilman 1997, Camill et al. 2004). Species group assignments for all species sown and encountered during the study are provided in Appendix C. To estimate ANPP as an index of ecosystem functioning, we clipped aboveground biomass to a height of 1 cm in September 2009 and 2010 from 0.5-m<sup>2</sup> quadrats placed where we had previously estimated cover and richness. Biomass produced in the current season was sorted in the field to remove the previous season’s litter and dried for 48 hours at 60°C prior to weighing. We did not separate biomass by species. In 2010, we sampled quadrats on the remaining complementary diagonal within each 1-m<sup>2</sup> subplot to avoid resampling where biomass harvests had occurred.

### *Calculation of Resistance, Recovery, and Resilience*

While resistance most often refers to the ability to withstand perturbation relative to steady-state conditions, these restorations may not have achieved steady state. Therefore, we defined resistance as the difference in seeded species cover or biomass between drought and control subplots within seeding treatments during the year of the drought treatment (2009). Similarly, we define recovery using differences in seeded species cover or biomass between drought (2009) and post-drought years (2010), and resilience, which combines resistance and recovery, as the ratio of post-drought (2010) to control (2010) seeded species cover or biomass. Hence, these parameters reflect changes with respect to a trajectory of establishment rather than

a steady state and integrate vegetation response during drought and the post-drought season, respectively. Resistance and recovery were calculated in proportional terms (following van Ruijven and Berendse 2010), because absolute resistance and recovery are correlated with pre-drought values. Proportional resistance was calculated as the difference in natural logs of seeded species cover or biomass between drought and control subplots. Proportional recovery was calculated as the difference in log seeded cover or biomass between post-drought and drought years.

### *Statistical Analysis*

We used repeated-measures mixed-model analysis of variance (ANOVA) to test responses of cover and richness to seed mixture richness, seeding density, and drought with year as a repeated measure on rainfall manipulation subplots within each whole plot. Whole plot within seeding treatment combination, plot row, and plot column were random effects. Mixed-model ANOVAs were performed in SAS version 9.2 (SAS Institute 2010) using PROC MIXED with Tukey-Kramer's adjustment for interaction contrasts and the Kenward-Roger method for degrees of freedom estimation. Full model outputs and treatment main effect means are presented in Appendix B. Separate treatment variance estimates were used in cases of heterogeneous variances (Levene's test). We used nonmetric multidimensional scaling (NMDS) with Ruzicka (quantitative Jaccard) dissimilarity matrices based on peak canopy cover to visualize differences in sown and non-seeded community structures separately within years with function "metaMDS." We assessed significance of factors (seed mixture richness, seeding density, and drought) in ordinations using permutation tests executed by function "envfit" in the VEGAN package (Oksanen et al. 2010) in Program R version 2.11.1 (R Development Core

Team 2010). Ordinations represent structural rather than compositional changes, because Ruzicka dissimilarity is based on relative cover rather than presence/absence data.

## Results

### *Establishment and Absolute Drought Effects*

*Species richness*—We encountered 37 seeded species over two seasons of sampling, with 15, 12, 26, and 26 total seeded species encountered among LR/LD, LR/ HD, HR/LD, and HR/HD whole plots, respectively. Seeded species richness at the 0.5-m<sup>2</sup> scale was greater in HR and HD treatments, and there was no evidence for interaction between seed mixture richness and seeding density (Fig. 3-1a). There was no significant effect of drought on seeded species richness (Fig. 3-1a), nor were there two- or three-way interactions between drought and seeding treatments (PROC MIXED; all  $P \leq 0.05$ ). Of all the species seeded exclusively to HR plots, *Helianthus maximiliani* Schrad. was the only species encountered on every HR plot in both years. Other examples of frequently encountered sown taxa included *Sorghastrum nutans* (L.) Nash, *Elymus* sp. (L.), *Astragalus canadensis* (L.), and *Andropogon gerardii* (Vitman).

We encountered 28 non-seeded species; 16 were annual or biennial and 16 were exotic (11 of 16 exotics were annual or biennial). Exotic richness was lower on HR and HD treatments, and there was no interaction between seeding richness and density (Fig. 3-1b). There was no significant effect of drought on exotic richness (Fig. 3-1b), nor were there two- or three-way interactions between drought and seeding treatments (PROC MIXED; all  $P \leq 0.05$ ). Examples of frequently encountered exotic taxa included *Conium maculatum* (L.), *Carduus nutans* (L.), and *Melilotus officinalis* (L.) Lam.

*Cover and ANPP*— Seeded species cover was greater and exotic species cover was lower in HR compared to LR treatments and in HD compared to LD treatments (fig. 3-1c, d). Seeded species cover was also greater on subplots not subjected to drought across seeding treatments (fig. 3-1c). There was a significant interaction between drought and year for exotic cover and for the combined cover of all annual / biennial species (PROC MIXED: Drought  $\times$  Year,  $F_{1,40}$ , both  $p < 0.01$ ), with increases from 2009 to 2010 restricted to the drought treatment (2009 to 2010 cover differences: control subplots; 2.70<sub>exotic</sub>%, 4.53<sub>ann/bien</sub>%, both  $p > 0.70$ , drought subplots; 14.99<sub>exotic</sub>%, 17.53<sub>ann/bienn</sub>%, both  $p < 0.01$ ). No other interactions between seed mixture richness, seeding density, drought and year were significant for seeded, exotic and annual/biennial cover (Proc Mixed, all  $p > 0.05$ ). Different components of seeded plant communities exhibited divergent responses within the experiment. Forb and C<sub>3</sub> graminoid cover were greater on HD plots, but only forbs had greater cover on HR plots (Table 3-1). Drought significantly reduced C<sub>3</sub> graminoid cover but not that of other groups (Table 3-1). The high cover of *H. maximiliani* on HR plots was obvious in the field, and *H. maximiliani* had the highest mean cover among all species (cover = 43.8%  $\pm$  3.84% [mean  $\pm$  SE]) on HR plots, which was similar to the combined cover of seeded graminoids (cover = 42.3%  $\pm$  11.58%) and all non-*H. maximiliani* forbs combined on HR plots (cover = 33.1%  $\pm$  6.40%). Despite high cover of *H. maximiliani* on HR plots, the combined cover of other seeded forbs was also greater on HR than LR plots ( $F_{1,12} = 11.01$ , mean cover difference = 16.9%,  $P = 0.02$ ). Patterns of ANPP were incongruous with the cover of seeded species in response to seed mixture richness, with less aboveground biomass produced annually on HR plots ( $F_{1,16.9} = 10.90$ , mean difference = 216.68 g $\cdot$ (0.5 m<sup>2</sup>)<sup>-1</sup> $\cdot$ yr<sup>-1</sup>,  $P < 0.01$ ), while main effects for drought, density, year, and all possible interactions were not significant (all  $P < 0.05$ ).

### ***Drought Resistance, Recovery, and Resilience***

There was little evidence for differential proportional resistance, proportional recovery, or resilience among seeding treatments for ANPP and seeded cover (Fig. 3-2), although the LD treatment had marginally lower seeded cover resistance and resilience (Fig. 3-2b, f). The LR/LD treatment combination exhibited resistance and recovery values significantly different from zero for seeded cover and ANPP, respectively (Fig. 3-2b, c), which indicate lack of resistance in terms of seeded cover and an increase in ANPP following drought. Resilience, measured within whole plots as the ratio of drought to control subplot biomass and seeded cover, was significantly less than one for the LR/LD treatment combination for seeded cover (Fig. 3-2f), so recovery was not sufficient on LR/LD plots to bring seeded species cover after drought back to levels observed on control subplots in 2010.

### ***Community Structure***

Community structure for seeded species differed among HR and LR plots, but was not affected by drought or seeding density (Fig. 3-3a, c), and drought consistently had no effect on community structure when tested within seed mixture richness treatments within years (envfit; all  $P > 0.2$ ). In ordinations, seeded species were those included in either HR or LR mixtures, so HR and LR treatments should differ in community structure, because the HR treatment utilized additional species. For example, *H. maximiliani*, which was only included in HR mixtures, was negatively correlated with the first axis (envfit;  $r^2=0.68$  for both 2009 and 2010,  $P < 0.01$  for both 2009 and 2010). Seed mixture richness but not drought or seeding density (both among and within density treatments) affected non-seeded species (exotics + native weeds) community structure in both years (Fig. 3-3b, d).

## Discussion

Our study is among few that demonstrate richness mediated enhancement of native plant community establishment and reduction of exotic cover on grassland experimental plots initiated using the common restoration practice of broadcast seeding, with neither tight control of community composition (e.g., Tilman 1997, Biondini 2007, Fornara and Tilman 2009) nor the use of small plots (<10 m<sup>2</sup>, e.g., Piper et al. 2007). Our findings also lend support for the applicability to restoration of some, but not all, results from more rigidly controlled experiments. For example, Piper et al. (2007) investigated the effects of seeding richness on establishment of seeded plant communities, but with a lower species richness gradient (1–16 species) in an experiment where mowing was used to control weeds. They reported that the benefits of richness saturated at eight species, but our findings suggest that higher levels of species richness may considerably enhance the establishment of seeded species cover and reduce exotic species cover in restorations, although the incremental benefit of each additional species may be small. Despite these benefits, we did not find strong evidence for differential drought resistance, recovery, or resilience among seeding treatments, although diminished resistance and resilience were detected for restoration plots that were LR/LD. This calls into question the ability of common seeding methods to modulate the robustness of restorations to projected climate change absent the targeted use of species or ecotypes with drought resistance or resilience traits.

### *Seeding treatments and establishment*

The practice of HD seeding and the use of HR mixtures had similar, but not interactive, effects on the establishment of seeded and exotic species richness and cover. Both of these methods enhanced establishment of seeded species and reduced the establishment of exotic species cover and richness. Their similar effects suggest that where available seed richness is



limiting, seeding at high density may provide alternative means of achieving desired results and vice versa. Because HR and HD plots both had greater small-scale richness than LR or LD plots, complementary resource use patterns or sampling effects could explain greater restoration establishment and enhanced exotic control from HR and HD mixtures. However, shifts in non-seeded community structure in response to seed mixture richness, and not seeding density, suggest seeded species had differential effects on species within the non-seeded community. Greater establishment of seeded species and reduced exotic cover are also consistent with priority effects (D'Antonio et al. 2001, Ejrnaes et al. 2006), if more seeded, native vegetation was able to establish early over more area relative to exotic vegetation on HD plots. At lower seed mixture ratios of grasses to forbs, Dickson and Busby (2009) showed poor forb establishment. Here, greater forb cover may have established on HR plots and supported greater overall establishment of cover for several non-mutually exclusive reasons. The HR mixture may have contained additional forbs that were relatively good competitors for resources with grasses in the seed mixtures or with non-seeded species (sampling effect, e.g., Huston 1997), had complementary patterns of resource use (e.g., Fornara and Tilman 2009, Marquard et al. 2009), or were good colonizers of open space at the outset (e.g., Ejrnaes et al. 2006). For example, a large portion of forb cover on HR plots was *H. maximiliani*, the rhizomatous spread and tall stature of which may have contributed to an ability to quickly cover bare ground (e.g., Burke and Grime 1996), gather resources, and contribute to the high overall cover of native, seeded species and reduced cover of exotic species.

Taken at face value, low ANPP on HR plots is surprising. However, HR plots had lower exotic species cover. Had we separated biomass into seeded and non-seeded species (which includes exotics), we may have observed different patterns for the subset of seeded species. We

expect that non-seeded species as a group allocated proportionately more of their biomass to aboveground structures relative to predominantly perennial seeded species, because most were annuals or biennials, whose lifetime fitness depends on the production of aboveground reproductive structures in one or two growing seasons (Monk 1966, Hautek ete et al. 2001). In contrast, many perennial grassland species, particularly C<sub>4</sub> grasses, have high ratios of belowground to aboveground biomass allocation (Risser et al. 1981). Using an estimate of ANPP as an index of ecosystem functioning may be less informative than an estimate of NPP that incorporates both belowground and aboveground allocation where plant above- and belowground allocation patterns are divergent (Kahmen et al. 2005, Wilsey and Polley 2006).

### *Drought effects*

The lack of clear effects of richness on drought resistance, recovery, and resilience, despite concurrent enhanced seeded species cover on HR and HD plots, contrasts with other grassland observational and experimental studies (i.e., Frank and McNaughton 1991, Tilman 1996, Picasso et al. 2010), and could result from several mechanisms. Seed mixture richness and seeding density treatments would have similar drought responses if the shelters failed to create stressful environments relative to control plots. We believe that the shelters were effective because we observed reduced 30-cm volumetric soil water content (see *Methods*) on drought subplots, coupled with reduced seeded cover, and increased exotic and annual/biennial cover following drought. However, simulated drought was not intense enough to cause decreases in seeded species richness or shifts in plant community structure. Given the reduced absolute cover of seeded species we observed in response to drought, the similarity in seeded community structure between shelters and controls at both levels of seed mixture richness suggests a lack of sufficient differential species responses to stabilize seeded cover, even at high richness. This

absence of shifts in community structure, which should occur if drought-tolerant species become relatively more abundant, precludes an important potential mechanism for diversity-enhanced stability (Tilman 1996, Loreau 2000, De Boeck et al. 2008). Diversity dependent production patterns may explain the lack of enhanced resistance to drought on HR relative to LR plots. More productive plant communities may have a greater chance of losing their growth potential under drought (Pfisterer and Schmid 2002), or have increased water consumption, leading to stress and mortality (Van Peer et al. 2004, Wang et al. 2007, Zavalloni et al. 2008). The higher total ANPP we observed on LR plots reduces the likelihood that these mechanisms explain our results. While there were not significant differences among seeding treatment combinations in terms of ANPP and seeded cover stability, the LR/LD seeding treatment combination did exhibit recovery in ANPP, but a lack of seeded cover resistance and resilience with respect to controls. There was also marginal evidence for reduced seeded cover resistance and resilience from LD plots. This could result from lower 0.5-m<sup>2</sup> seeded richness on LD plots, or suppression of seeded cover resilience by exotics. The latter would agree with the uniform resilience observed for ANPP, which, unlike seeded cover, included exotic biomass from mostly annual/ biennial species. The potential that local trait variation, here trait variation among species establishing from seeding mixtures, within either species or ecotypes, may be insufficient to buffer native communities and ecosystems against, or promote recovery from, global change generally and climate change specifically, has received increasing attention over the past decade (Wilkinson 2001, Seastedt et al. 2008), and should be the focus of experimental study. Invasion opportunities have been linked to global warming (Walther et al. 2009), but increased cover of exotic species across seed mixture richness and seeding density treatments during the year following drought links exotic response and climate change more generally. Annual and biennial plants tend to be associated

with disturbance (McIntyre et al. 1995), so the increase in annual/biennial cover after drought along with the annual/biennial habit of most exotic species at our site may explain their ability to respond quickly relative to predominantly perennial-seeded species. In tallgrass prairie, recruitment for perennial vegetation draws largely from belowground buds produced during the previous growing season rather than seed banks (Benson and Hartnett 2006), which may limit the ability of native perennial species to respond to disturbances that occur over relatively short time scales. In that sense, exotic species may have enhanced biomass recovery and resilience by their presence, because they were capable of rapid demographic response. Van Ruijven and Berendse (2010) observed increasing resilience as a function of richness. While we did not observe this pattern, our results are less contradictory if the response of exotic species is considered. Targeting native annual and/or biennial species for inclusion in seed mixtures may be useful for increasing trait variation. This may enhance recovery and resilience over time scales similar to that of this study via increases in a native subset of the plant community in the post-drought environment, which might otherwise support an enhanced response by exotic annual and biennial species.

### *Conclusions*

We recommend the use of HR and HD methods and suggest that these may be substitutable if either diversity or density alone are limiting, particularly where the establishment of small-scale species richness, native species cover, and low exotic species cover are restoration targets. Positive effects of high seeding density on native vs. exotic cover and richness were still evident four to five years after the initial seeding. We caution, however, that HR plots may have greater richness at larger spatial scales than HD plots. Larger-scale richness driven by rare species likely represents much of the species pool (*sensu* Zobel 1997) available for response to

long-term biotic and abiotic changes on these plots, and this warrants consideration with respect to restoration targets. High richness at greater spatial scales should be more important, particularly for sites expected to have greater longevity. Productivity responses, while statistically discernible, were unexpected and difficult to interpret in the context of seed mixture richness, and would yield inferences opposite to that from patterns of seeded species cover, if taken at face value. We recommend separate analysis of seeded species contributions to ANPP or estimation of combined above- and belowground NPP for inference of seeding richness effects on the restoration of ecosystem function. Neither HR nor HD treatments produced plant communities with superior drought resistance, recovery, or resilience, which may be important properties for restored grasslands given projected increases in drought frequency and severity. The insurance hypothesis predicts that diverse communities should be more likely to contain species that will compensate for others in response to perturbation (Yachi and Loreau 1999). In our case, greater representation of native annual/biennial species or species known to have drought tolerance traits in seed mixtures may confer greater stability to a one-year drought, and this should be evaluated in future studies. Trade-offs between resistance and resilience traits may be diminished, if resilient species primarily exist in seed banks during non-recovery years. More generally, other methods to modulate trait variation or introduce traits (e.g., through managed relocation) tailored to stabilizing restored plant communities in response to specific perturbations and possible drawbacks of such methods should be foci of restoration research.

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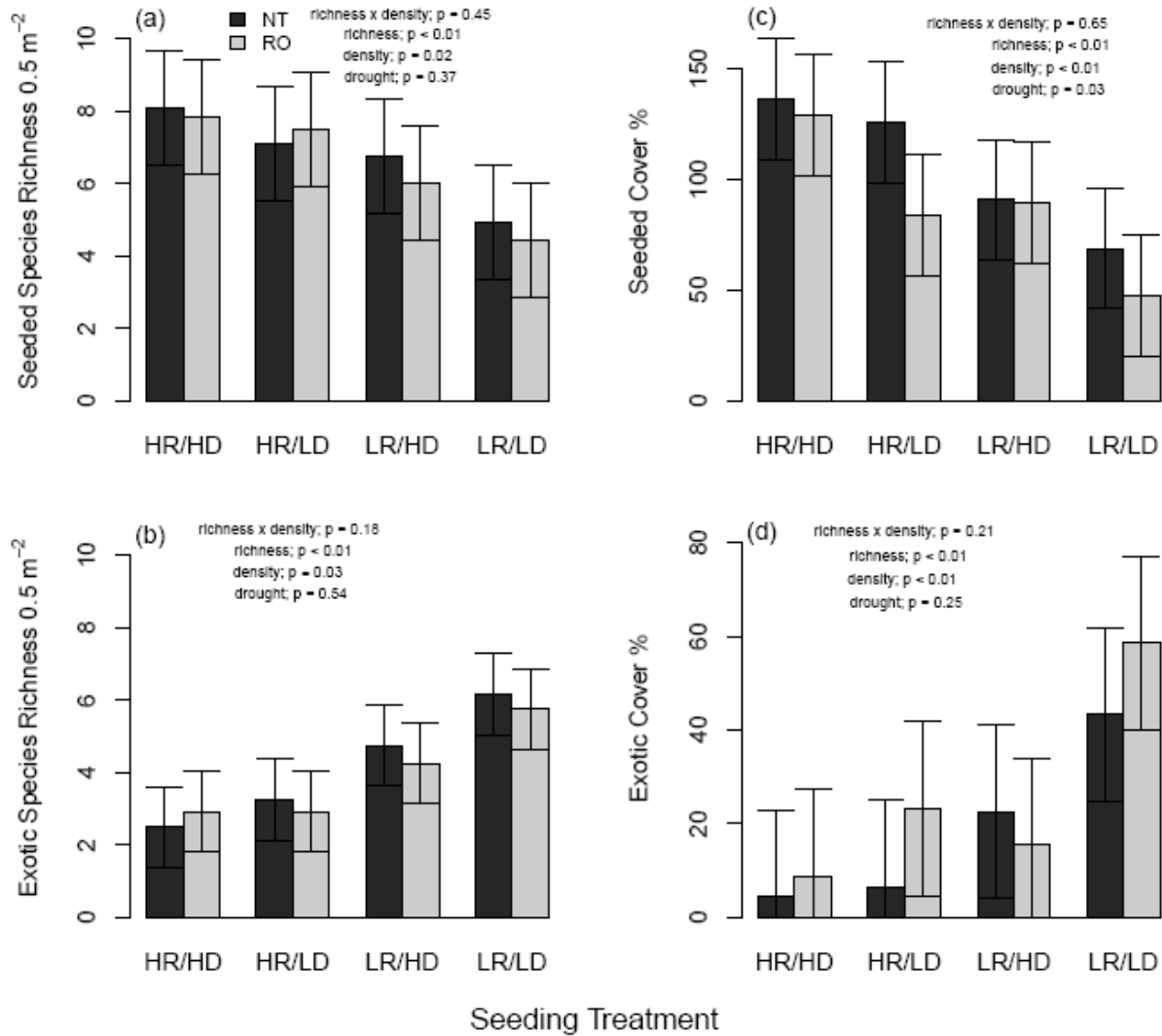
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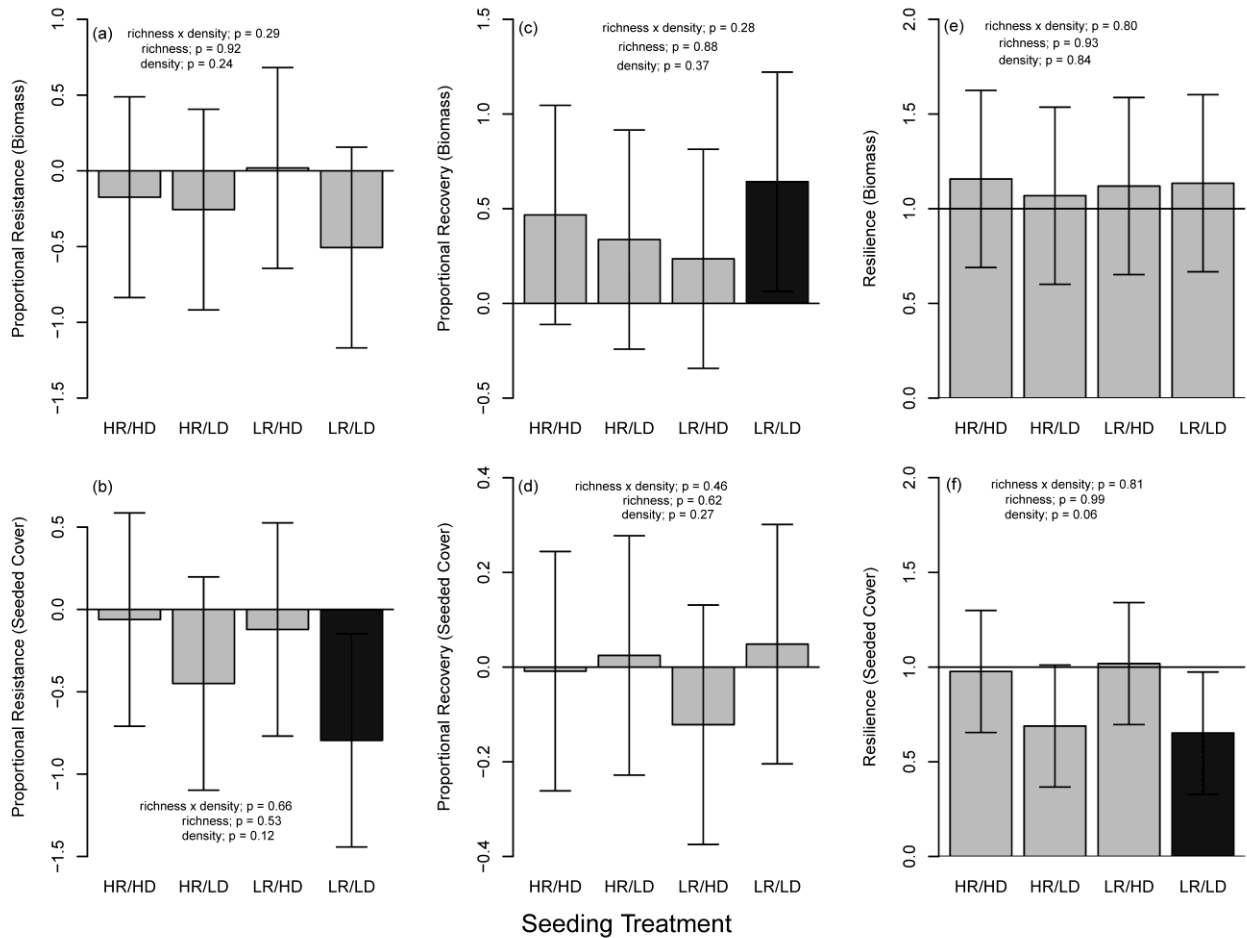
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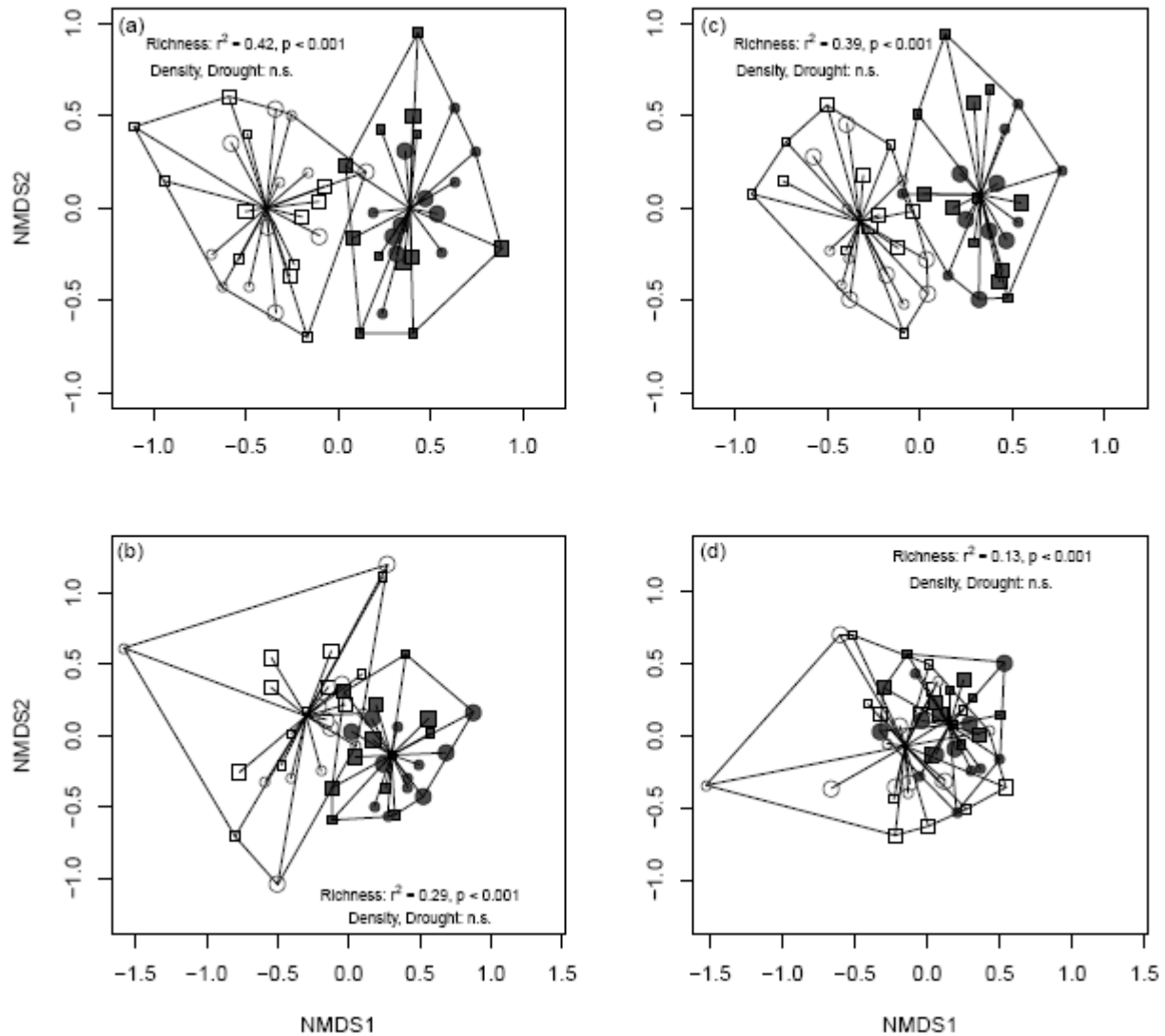
## Figures and Tables



**Figure 3-1.** Mean species richness by seeding treatment combination on drought (RO) and control (NT) subplots for (a) seeded species and (b) exotic species, and mean cover by seeding treatment on RO and NT subplots for (c) seeded species and (d) exotic species. Significance values are provided for the seeding richness, density, and drought main effects and the richness × density interaction. All error bars represent mean ± SE. Treatments are HR, high richness; LR, low richness; HD, high density; LD, low density. Means, standard errors, and levels of significance are from PROC MIXED repeated-measures ANOVA.



**Figure 3-2.** Proportional resistance (a-b), proportional recovery (c-d), and resilience (e-f) by seeding treatment combination for biomass (top row) and seeded species cover (bottom row)  $\pm 2$  standard errors. Treatment coding follows fig. 3-1. Significance values are provided for seeding richness and density main effects and their interaction, and significant differences from zero for treatment combinations (a-d) and one (e-f) are indicated by dark bars. Means, standard errors, and significance values are from Proc Mixed repeated measures ANOVA.



**Figure 3-3.** NMDS ordinations for plant community structure with correlation coefficients and p-values (Envfit permutation tests) for single treatment factors explaining fit for seeded species only in 2009 (a) and 2010 (c) and for non-seeded species only in 2009 (b) and 2010 (d). Lines connect points (both levels of drought and seeding density treatments within HR and LR treatments) to HR and LR centroids and form perimeters around HR and LR groups. Symbols: gray = HR; white = LR; circle = HD; square = LD; large = drought; small = no drought. Stresses (a-d) respectively = 22.45, 22.52, 22.62 and 23.5).



**Table 3-1.** Significance of treatments with mean differences and standard error (where significant) for cover of functional groups included in seeding mixtures.

Functional Group	Seed Mixture Richness	Seeding Density	Rainfall Manipulation
C <sub>4</sub> grasses	n.s.	n.s.	n.s.
C <sub>3</sub> graminoids	n.s.	HD>LD *, 11.57(3.84)	Control > Drought *, 9.56(3.94)
Forbs	HR >LR **, 57.74(5.35)	HD>LD *, 14.41(5.35)	n.s.

*Notes:* Significance coded:  $p < 0.005$ , \*\*,  $p \leq 0.05$ , \*;  $p > 0.05$  n.s. Group with greater mean value (%) indicated, followed by mean difference and s.e. in parenthesis (Proc Mixed repeated measures ANOVA).

## Chapter 4 - Drought-mediated stem and below-ground bud dynamics in restored grasslands<sup>3</sup>

### Abstract

**Question:** Does the below-ground bud bank mediate response to drought in restored grasslands?

**Location:** Platte River Valley region of south-central Nebraska, USA.

**Methods:** We imposed severe drought for one growing season using rainfall manipulation structures and measured the response of above- and below- ground plant communities (ramet and below-ground bud densities) with respect to non-drought controls during the drought year and a recovery year.

**Results:** Drought reduced below-ground bud bank density and above-ground stem density. However, bud bank density recovered, and bud production was higher on previously droughted subplots relative to controls in the year following drought. The response of below-ground bud and above-ground stem density to drought differed according to functional identity ( $C_3$  grass,  $C_4$  grass and forb), with forbs least resistant to, but having the greatest recovery from, drought.

**Conclusions:** While overall density in restored grasslands was resilient, drought effects on below-ground bud banks may have longer-term impacts on plant community structure. Reduced density above- or below-ground during the growing season following drought may allow for the persistence of species relatively more reliant on recruitment from seed banks in favourable micro-sites.

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<sup>3</sup> Reprinted with permission from Wiley Publishing: “Drought-mediated stem and below-ground bud dynamics in restored grasslands” by D.L. Carter, B.L. VanderWeide, & J.M. Blair, 2012. *Applied Vegetation Science*, 15, 470-478.

## Introduction

Habitat loss exceeds protection in remaining temperate grasslands more than in any other biome (Hoekstra et al. 2005). In North America, restoration of grasslands via the reintroduction of native vegetation to ex-arable lands has gained momentum since the 1960s (Cottam & Wilson 1966; Mlot 1990). Remnant grassland losses and increasing grassland restoration activities have elevated the importance of restored grasslands for the maintenance of biodiversity and ecosystem functioning in the future. However, most current research on disturbances in grasslands utilizes remnant or semi-natural grasslands (e.g. Noymeir 1995; Hartnett et al. 1996; Baer et al. 2005; Yahdjian & Sala 2006; Fiala et al. 2009; Chimner et al. 2010), while responses of young, restored grasslands to disturbance remain relatively unexplored and poorly understood. Mid-continental regions, where most grasslands are found, are generally expected to experience increased risk for drought over the coming century (Meehl et al. 2007). Central North American grasslands have frequently experienced drought on annual and decadal time scales over the past millennium (Stambaugh et al. 2011), and extreme drought events are predicted to increase in frequency within decades (Strzepek et al. 2010). The effects of drought in temperate grasslands are diverse, including changes in community composition and structure (Weaver et al. 1935; Kennedy et al. 2003), decreases in primary productivity (Fay et al. 2003; Kennedy et al. 2003; Gilgen & Buchmann 2009) and shifts in biomass allocation patterns within species (Weißhuhn et al. 2011).

Although drought reduces individual plant growth and alters community structure, some effects of drought on grassland plant communities may be explained by responses of the below-ground bud bank. The below-ground bud bank, first broadly characterized by Harper (1977), consists of dormant meristems of perennial grasses and forbs that are produced in the leaf axils

of phytomers during the growth of rhizomes and other below-ground stems (Briske 1991; Moore et al. 1991). Harper's definition of buds has more recently been expanded to include 'all buds that can potentially be used for vegetative regeneration,' including buds that form adventitiously from roots (Klimešová & Klimes 2007). Although below-ground bud viability declines substantially over time for some grassland species (Henderson & Briske 1997), buds of the perennial C<sub>4</sub> grass *Andropogon gerardii*, an abundant native in North American tallgrass prairies, may persist on the rhizomes of parent plants for 3 or more years (Ott & Hartnett 2011). As a result, bud banks can be an important source for regenerating vegetation above-ground following disturbance in perennial-dominated systems (Rogers & Hartnett 2001; Dalglish & Hartnett 2006; Klimešová & Klimes 2007). In mesic remnant grasslands in central North America, nearly all above-ground stems are recruited from the below-ground population of reserve meristems rather than the seed bank (Benson & Hartnett 2006). The bud bank in young, restored grasslands may contribute relatively less to recruitment of above-ground stems because the density of native perennial species remains low and recruitment micro-sites for seeds are still abundant. Despite its low density, the bud bank could still play an important role in the drought response of newly restored grasslands by buffering responses of established plants to disturbance and facilitating establishment and clonal spread of native vegetation.

While we are aware of no studies concerning the effects of environmental perturbations on bud banks in restored grasslands, several studies have described how the effects of disturbances, such as fire and grazing, are mediated through the bud bank in field experiments (Busso et al. 1989, Dalglish & Hartnett 2009). Fire removes litter and existing vegetation (Hulbert 1969). Removal of phytomass increases the quantity of light that reaches the soil surface, warming it (Knapp et al. 1998), and alters the incident red:far-red light ratio

(Willems 1983). Increased red:far-red light ratios (Tomlinson & O'Connor 2004) and increased soil temperatures (Svejcar 1990) are potential cues for the growth of buds into tillers. The resulting highly productive, dense population of above-ground stems in recently burned areas replenishes the bud bank (Benson et al. 2004). Responses to disturbance may differ among functional groups, depending on the timing and severity of the disturbance (Klimešová & Klimes 2007; Dalgleish & Hartnett 2009). This suggests that functional groups that are more able to either conserve buds during drought or produce new buds in spite of drought may contribute more to post-drought recovery in perennial-dominated grasslands.

To investigate the effects of drought on stem and bud dynamics in young, restored grasslands, we utilized restoration plots sown in 2006 by The Nature Conservancy (TNC) in south-central Nebraska, USA. We experimentally imposed severe drought during the 2009 growing season and tracked below-ground bud densities and aboveground stem densities of sown, native species on drought and control subplots during the drought year (2009) and a recovery year (2010). The following questions guided our research: (1) does drought affect above-ground stem density during the drought year? Emergence of most species may occur before the realization of drought stress, causing stem density to be initially independent of drought. (2) Are below-ground bud densities and numbers of buds per stem reduced on drought subplots relative to controls receiving ambient rainfall? Drought can decrease belowground productivity in grasslands (Frank 2007), which may be associated with reduced numbers of phytomers and attendant buds, or a reduction in phytomer size with no change in bud numbers. (3) Are there lagged effects of drought on above-ground stem and below-ground bud density? (4) Do bud and stem dynamics of particular functional groups ( $C_4$  grasses,  $C_3$  grasses and forbs) differ in their responses to drought? Species or functional groups could respond differently to

drought because of differences in drought tolerance and growth phenology (Kassioumi et al. 2002; Tucker et al. 2011). This research will help us better understand the effects of growing season drought on grassland restoration establishment and determine if below-ground bud banks are involved in response to drought.

## **Methods**

### ***Study area***

We imposed drought treatments within a grassland restoration experiment at a TNC site in south-central Nebraska, USA (40°41'N, 98°35'W). The experimental plots cover 34.4 ha in an area tilled annually for intensive *Zea mays* production through 2005, so we assume little, if any native vegetation was present prior to initiation of the experiment. Soils consist of loams and loamy sands over deeper coarse sands (Bolent-Calamus complex, Caruso loam, Gothenburg loam, Wann loam). The climate is continental with a mean annual temperature of 10.4 °C and mean annual precipitation of 629 mm (both 1971-2000 means), 65 % of which falls between 1-May and 30-August (United States Historical Climate Network, USHCN). Precipitation totals for 2009 and 2010 were 615 and 683 mm respectively (USHCN, National Weather Service).

### ***Seeding and drought treatments***

The 24 experimental plots consist of square plots (0.3 ha each) with a factorial combination of two levels of seed mixture richness (high richness, HR = 95 species; low richness, LR = 15 species) and two levels of sowing density, yielding six replicates of each richness by density combination. Equal weights of bulk seed were sown among HR and LR plots, but HR plots had slightly higher sowing densities of pure live seed (tetrazolium test) than LR plots (low density, LD = 164 or 172 live seeds·m<sup>-2</sup> and high density, HD = 328 or 344 live

seeds·m<sup>-2</sup> for LR and HR respectively). All seeds were collected within the central Nebraska Platte River region and broadcast sown over damp soil and melting snow in late March and early April, 2006. While not the focus of this manuscript, seeding treatments were included as fixed effects in statistical analyses. These seeding treatment combinations were applied to plots in a systematic rather than random fashion, so we used row and column identifiers for plots as random effects in statistical analyses.

From mid-March through early-October 2009, we simulated severe drought with passive rainfall manipulation structures erected at random locations within each of 24 large seeding treatment plots. Shelters intercepted approximately 80% of ambient rainfall using a slight modification of the design proposed by Yahdjian & Sala (2002), whose shelters permitted greater than 90% transmittance of the visible spectrum, reduced soil volumetric water content (SWC) under shelters, but led to slightly cooler air and soil temperatures under the shelters. Briefly, shelter structures consisted of tubular metal frames with clear Lexan® plastic shingles bent lengthwise at 120° and secured to the frames to divert rainfall into a gutter, which carried water at least 1.5 m from shelter edges. Drainage was facilitated by sandy soils. Shingle material transmitted greater than 90 % of visible light. Shingles were spaced for 80% coverage of the 2.5 by 2.34 m<sup>2</sup> shelter area , which was not square due to a 15° tilting of the roof to divert water. The shelters were 1.5 m tall on their high side to minimize growth of tall vegetation through spaces between the shingles and each oriented with the high side facing away from prevailing summer winds to minimize the lateral intrusion of precipitation. Shelters were erected at least 15 m from plot edges within each of the 24 large seeding treatment plots. Drought subplots (1 m<sup>2</sup>) for sampling were established under the center of each shelter and control subplots (1 m<sup>2</sup>) receiving

ambient rainfall were established randomly either 1.5 m north or south of each shelter within each large seeding treatment plot.

To verify the effectiveness of the shelters, we monitored soil water content (SWC, 30 cm depth, time domain refractometry methods, CS616 soil moisture probes with CR10x data loggers from Campbell Scientific, Logan, UT, USA) for a 26-d period under the central 1 m<sup>2</sup> of one shelter. We observed a 30–60% reduction in SWC relative to soil measured 1.5 m from the shelter edge (side opposite that of gutter outflow) (Appendix B), which corroborates the findings of Yahdjian & Sala (2002). Reduced SWC at depth over this prolonged period makes us confident that shelters created a satisfactory drought treatment.

### *Stem and bud sampling*

We estimated stem density by species in May and August 2009 and 2010 from stem counts within two 0.25 m<sup>2</sup> quadrats arrayed diagonally within each 1-m<sup>2</sup> subplot sampling area. Peak density estimates for species across May and August sampling dates were used in statistical analysis. We combined density estimates from three species in the genus *Elymus* that had been included in restoration mixtures because we could not reliably identify small individuals to species in the field. To measure the density of the below-ground bud bank, we harvested 10 cm × 10 cm soil cores to a depth of 15 cm during the pre-drought, immediately post-drought and 1 yr post-drought dormant seasons. Sampling during the dormant season avoids the large fluctuations in bud densities that occur throughout the growing season, allowing comparison of bud densities among years (Dalglish & Hartnett 2006). Pre-drought cores were taken from a 6-m transects adjacent to future locations of drought treatment and control subplots (12 below-ground samples per transect taken at 0.5-m intervals, March 2009). Bud densities from these samples are presented as pre-drought baselines but not included in statistical analyses of drought effects,



because transects were from whole plots rather than subplots. We estimated below-ground bud density immediately post-drought (November, 2009) and 1 yr post-drought (November, 2010) using eight cores each per drought and control subplot. We used areas within subplots sampled the preceding season for stem density, thereby ensuring that the same area was sampled for both metrics and avoiding disturbance of areas used for stem counts in the following season. All below-ground samples were placed in plastic bags and stored at 4 °C pending processing (within 1 mo). Processing involved rinsing soil from the below-ground samples (no more than 2 wk prior to examination) and examining them using a dissecting microscope, trimming roots as necessary to allow thorough examination of the below-ground structures. Below-ground buds were counted and assigned to species when possible using bud morphology, phyllotaxy, morphology of the attached root system and morphology of any remaining above-ground parts. Buds from the genera *Helianthus*, *Solidago*, and *Elymus* were scored to genus, because identification of below-ground structures to species was not possible. Remaining individuals that could not be identified constituted a very small percentage of the total below ground bud bank (0.71%) and were excluded from analysis. As outlined in Dalglish & Hartnett (2006), buds of rhizomatous grasses and forbs are found at rhizome nodes and are easily visible. Buds of bunch grasses were counted by dissecting the base of each tiller. Most taxa produced buds at nodes, but two legumes (*Astragalus canadensis* and *Glycyrrhiza lepidota*) also produced buds adventitiously from roots. A list of species sown into and encountered in the experiment, with functional group designations, is given in Appendix B. All nomenclature follows the United States Department of Agriculture PLANTS Database (USDA-NRCS).

## *Statistical Analysis*

The TNC's initial motivation for this experiment was to investigate the consequences of two levels of restoration sowing density and two levels of seed mixture richness on the establishment of restored grasslands. However, the focus of our study was the response of grassland restoration plots to drought across treatments, although we modeled effects of these treatments in our analyses. We used repeated-measures mixed model analysis of variance (ANOVA) to test effects of drought, seed mixture richness, sowing density and year on bud density, stem density and number of buds per stem (bud density·m<sup>-2</sup>/stem density·m<sup>-2</sup>), with year as a repeated measure, on rainfall manipulation subplots within each whole plot. We used whole plots within seeding richness and sowing density treatment combinations and whole plot row and column identifiers as random effects. Repeated-measures mixed model ANOVAs were performed using Proc Mixed with Tukey-Kramer's adjustment to control family-wise error rate for interaction contrasts (significant or marginally significant interactions) and Kenward-Rogers degrees of freedom estimation. Distributions for all response variables were not significantly different from normal (Proc Genmod, chi-square test of fit), with the exception of buds per stem combined among functional groups. We modeled the latter, which was fitted by the gamma distribution, using a mixed model in Proc Glimmix (dist = gamma), but inference was identical to Proc Mixed, so Proc Mixed analysis is presented. We analyzed patterns for stems, buds and buds per stem for seeded species for three groups: C<sub>3</sub> grass, C<sub>4</sub> grass and forb, which have been defined as functional groups (sometimes 'guilds') elsewhere (Kindscher & Wells 1995; Tilman 1997; Camill et al. 2004). Analyses of buds per stem utilized only seeded species encountered both as buds and as stems over the course of the study. All analyses were performed in SAS®

version 9.2 (2002–2008; SAS Institute, Cary, NC, USA). We report all drought  $\times$  year interactions, and both drought and year effects where their interaction is not significant. Effects Drought and year effects were not contingent on density or richness for any response variable.

## Results

We encountered more taxa in our above-ground than below-ground sampling (33 vs 13), but 97% of above-ground stems belonged to taxa also encountered below-ground. All taxa encountered below-ground were encountered above-ground. Of below-ground buds pooled across treatments and years, 10% were from C<sub>3</sub> grasses, 31% were from C<sub>4</sub> grasses and 59% were from forbs. Of stems pooled across treatments and years for taxa also encountered as below-ground buds, 34% were from C<sub>3</sub> grasses, 40% were from C<sub>4</sub> grasses and 26% were from forbs.

### *Total buds and stems*

Below-ground bud density was reduced in response to drought during the dormant season immediately after drought, but there was no significant difference in bud density between control and drought subplots 1 yr later (Fig. 4-1a). Stem density increased from 2009 to 2010 on control but not drought subplots (Fig. 4-1b). There were no significant differences in stem density between drought and control subplots during the drought year, but drought subplots had lower stem densities than control subplots in the subsequent year (Fig. 4-1b). The number of buds per stem was lower on drought subplots in 2009 (Fig. 4-2). This effect was transient, as the number of buds per stem was marginally higher on drought subplots than control subplots during the recovery year (Fig. 4-2).

### *C<sub>3</sub> grass, C<sub>4</sub> grass, and forb responses*

The nature of above-ground stem and bud dynamics across years differed among functional groups (Fig. 4-3, Table 4-1). Increases in stem density across years were restricted to control subplots for C<sub>3</sub> grasses, but increases for forbs were neither contingent on drought treatment nor year (Fig. 4-3a,c). Increases in C<sub>3</sub> and C<sub>4</sub> grass bud density across years were not contingent on drought treatment, but the increase in forb bud density was restricted to drought subplots (Fig. 4-3d–f). With the exception of C<sub>3</sub> grasses, there was no evidence for differences in buds per stem either between years or between drought and control subplots for functional groups (Table 4-1). The number of buds per stem on drought subplots was higher for forbs than C<sub>3</sub> grasses in both years and higher than C<sub>4</sub> grasses in 2009 (Table 4-1).

### **Discussion**

Our study is among the first to demonstrate effects of drought on below-ground bud communities in restored grasslands. Below-ground bud density was reduced immediately following drought, and this pattern was consistent with the lagged effect on stem densities, which were reduced during the recovery growing season. The number of buds per stem on drought subplots was high relative to control subplots following the recovery year. This pattern, which could result from increased bud production or decreased bud mortality, also contributed to the resilience of below-ground bud bank density relative to controls. This suggests that occasional droughts of short duration ( $\leq 1$  yr) may do little to impede the recovery of native density in restored grasslands, as long as they do not occur during the initial recruitment of native vegetation (e.g. Hallett et al. 2011) or yield recruitment conditions that permit the establishment of exotic or other weedy species (Pérez-Fenéndez et al. 2000; Corbin & D'Antonio 2004). Stem recruitment was unaffected in the year of the drought, which agrees with the results of Busso et

al. (1989) for two desert grass species. This may have occurred because most stems emerged in spring before the drought could reduce soil moisture to a stressful level. We observed differential effects of drought among functional groups, which likely were important for the response of the combined bud bank. While stem densities of C<sub>3</sub> grasses, C<sub>4</sub> grasses and forbs were not reduced relative to controls during the drought growing season, only bud densities of forbs were significantly reduced immediately following drought. Reduced bud densities may cause forbs to contribute more to vulnerability to environmental change (e.g. Chapin et al. 1997) in this restored system. However, forb stem density on drought subplots matched that of controls the year following drought, and forb bud density exceeded control subplots following the post-drought growing season. Post-drought forb stem populations might have relied less on bud banks than grasses, because some perennial forbs maintain and utilize seed banks relatively more than perennial grasses for annual stem recruitment (Rabinowitz & Rapp 1980; Stampfli & Zeiter 2004). Seed banks might have buffered forb stem densities following drought, despite the initial reduction in forb bud density, contributing to subsequent recovery of both forb bud densities and the high bud production per stem at the community level. The observed forb bud density response illustrates how resistance and recovery can be divergent within functional groups in communities (e.g. Boucher et al. 1994; Bee et al. 2007), such that short- and longer-term shifts in community structure are opposite. Unlike forbs, both C<sub>3</sub> and C<sub>4</sub> grass stem densities were lower in 2010 following drought, and grass bud banks were not significantly reduced by drought in 2009 or 2010. Two explanations could address these patterns. First, smaller proportions of bud banks produced in 2009 may have emerged as stems in 2010, and the below-ground buds of grasses may persist across years, which would indicate that more species in our system behave like the species investigated in Ott & Hartnett (2011) than those investigated in Henderson &

Briske (1997). Second, bud production may have increased or mortality decreased following drought due to increased nitrogen availability (Cui & Caldwell 1997; Enquist et al. 1998). We believe the second explanation is more likely because Dalgleish et al. (2008) reported that bud production contributes substantially more to population growth rates in demographic models and that nitrogen addition can increase the number of buds produced per stem. However, it is not clear to what extent either current bud production or maintenance of and recruitment from older buds contributed to stem densities. Regardless, time lags in bud-mediated recovery may allow species to establish or persist that are less reliant on budbanks for population maintenance or more reliant on seeds for dispersal.

While the community structure of the below-ground bud bank often more closely matches above-ground community structure than the seed bank (Klimešová & Klimes 2007), we observed differences in the responses of functional groups above- and below-ground. These differences yield insights into the contributions of different functional groups to bud banks and the associated capacity of these restored grasslands to respond to perturbation. Tilman (1996) showed that differential responses within plant communities could stabilize overall dynamics. While the short-term response of forbs increased the effect of drought on overall density, forbs also attenuated the effects of drought on below-ground bud banks over longer periods. Both forbs and C<sub>4</sub> grasses may contribute more in an absolute sense to bud-mediated recovery of stem density after drought than C<sub>3</sub> grasses, because both make up larger fractions of the below-ground bud bank and forbs exhibited relatively high densities of buds per stem both immediately and 1 yr following drought.

While the below-ground bud banks of target vegetation recovered following drought in these restored grasslands, drought may still have appreciable long-term effects. Reductions in

bud density immediately after drought may reduce short-term above-ground recovery upon the return of more favorable conditions. Lagged effects on above-ground density could promote invasion or the persistence of existing exotic or ruderal species (e.g. Pérez-Fenández et al. 2000). Also, differential capacities for bud production or maintenance among functional groups could lead to more persistent changes in plant community structure. Here, forb stem density did not differ from controls on drought subplots in 2010, despite reduced bud densities immediately following drought. This, combined with increases in forb bud density per stem, contributed to the resilience of the combined bud bank. Forbs may persist for longer periods, even in the presence of superior competitors, if they are more able to pre-empt space following drought or other disturbances (e.g. D'Antonio et al. 2001; Ejrnaes et al. 2006).

The lack of lagged effects of drought on forb stem density also highlights how seed banks may be an important means by which vegetation exploits available space and resources in this system (e.g. Aboling et al. 2008), but we cannot address whether stem densities for forbs and other vegetation in 2010 were driven more by an increase in proportional bud recruitment to stems from a depleted bud bank or recruitment from the seed bank. Future work should relate the importance of seed vs. bud banks to both timing and extent of recovery, community structure and potential impacts for delayed recovery for ecological processes.

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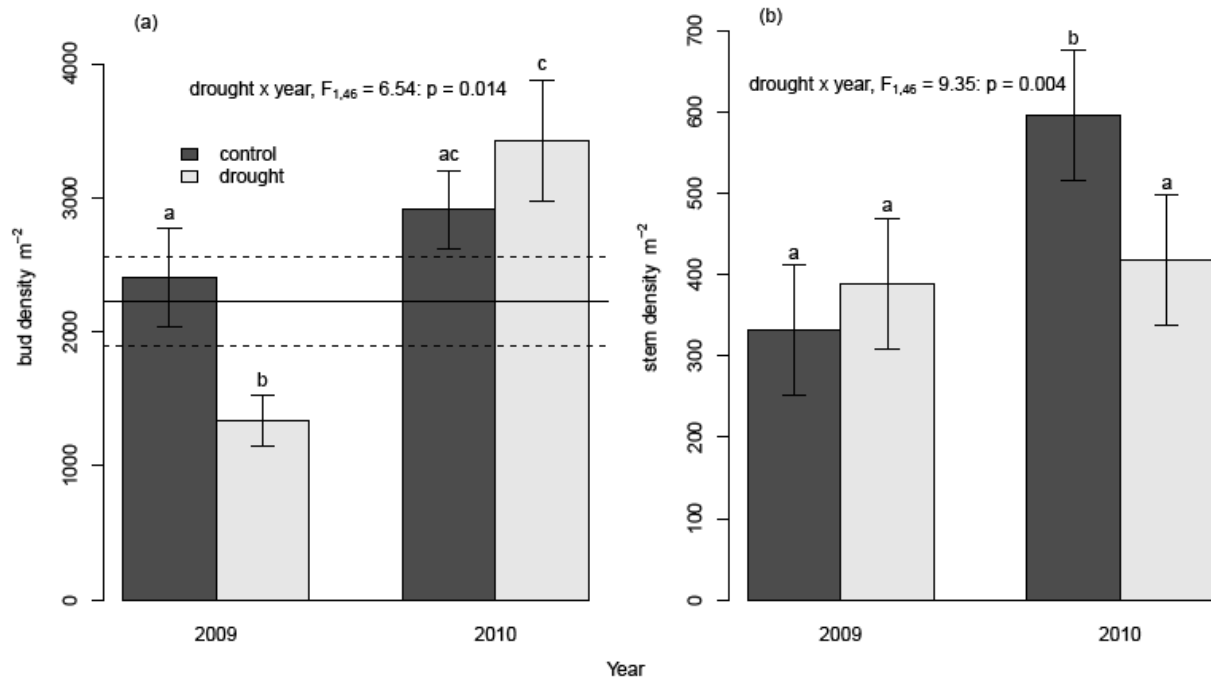
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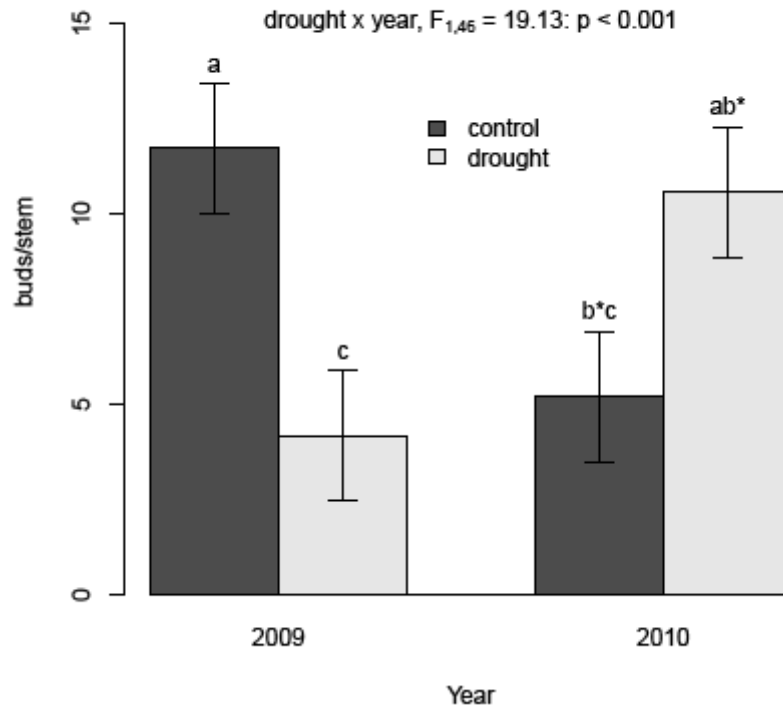
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## Figures and Tables

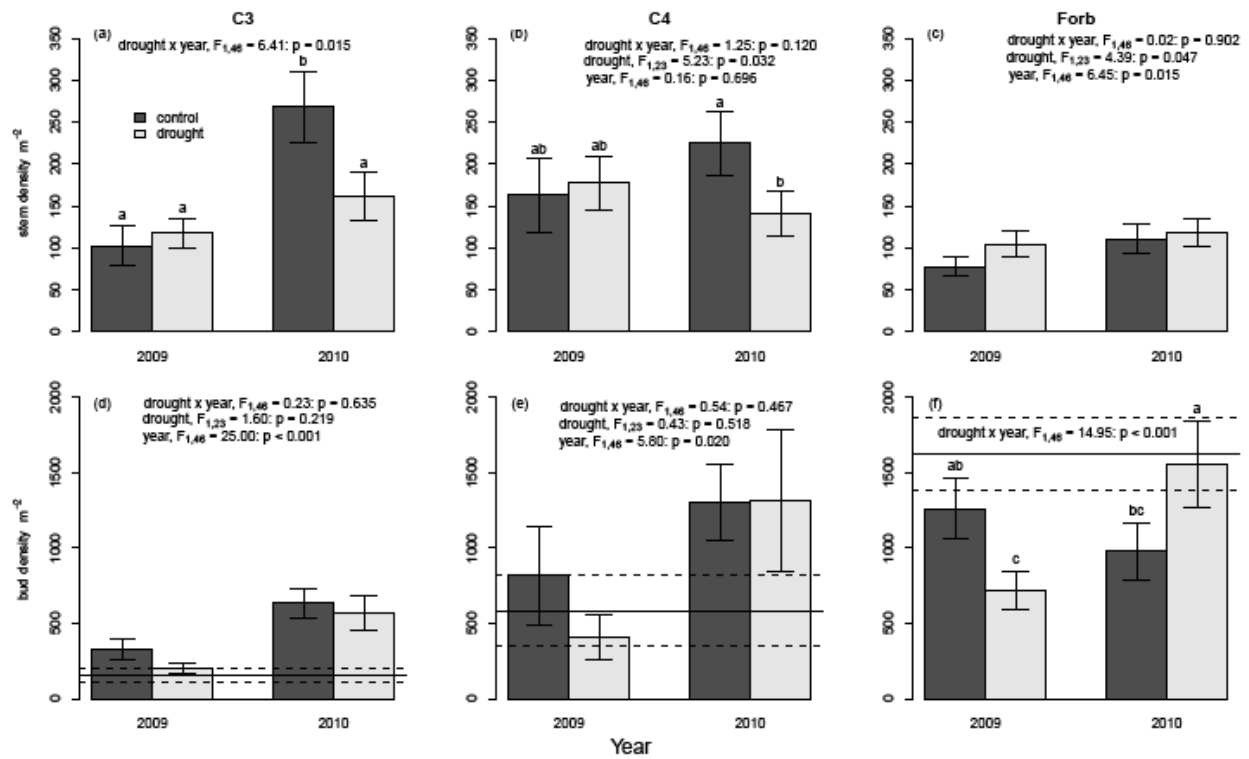


**Figure 4-1.** (a) Bud densities from the dormant season immediately after drought (2009) and 1 yr after drought (recovery, 2010) for control and drought subplots (see legend) with reference pre-drought (2008) mean bud density  $\pm$  SE indicated by the solid horizontal and dashed lines, respectively. (b) Stem densities from drought (2009) and recovery (2010) growing seasons. (a & b) Letters indicate significant ( $P \leq 0.05$ ) Tukey-Kramer adjusted interaction contrasts. Drought  $\times$  year interaction statistics: Fixed Effect, F-statistic numerator DF, denominator DF: P-value.



**Figure 4-2.** Bud density divided by stem density for drought (2009) and recovery (2010) years for control and drought subplots (means  $\pm$  SE). The asterisk denotes a contrast with  $P = 0.064$ . Otherwise, contrasts and statistics follow Fig. 4-1.





**Figure 4-3.** Stem density (a–c) and bud density (d–f) responses for 2009 and 2010 among C<sub>3</sub> (a,d), C<sub>4</sub> (b,e) and forb species (c,f) for control and drought subplots, all means  $\pm$  SE. Horizontal lines, contrasts and statistics follow Fig. 4-1.

**Table 4-1.** . Estimated buds per stem means  $\pm$  SE and indication of significant differences from Tukey-Kramer adjusted contrasts within functional groups (uppercase) and among functional groups (lowercase) within drought  $\times$  year combinations. The final row combines years and drought treatments within whole plots. Drought  $\times$  year combinations where buds but not stems were encountered were assigned ‘NA’ for analyses due to zeros in denominators ( $\leq 7/24$  values for any drought 9 year combination).

Year	Drought	C <sub>3</sub> Grass		C <sub>4</sub> Grass		Forb	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
2009	No	12.7 (A, a)	2.2	17.2 (A, a)	5.3	18.4 (A, a)	3.8
2010	No	3.0 (B, a)	2.1	9.9 (A, a)	4.8	12.3 (A, a)	3.7
2009	Yes	2.4 (B, a)	2.1	2.6 (A, a)	5.1	9.4 (A, b)	3.7
2010	Yes	4.7 (B, a)	2.1	7.6 (A,ab)	5.6	15.5 (A, b)	3.7
<b>COMBINED</b>		5.5 (a)	1.4	9.3 (ab)	2.5	13.9 (b)	2.7

## Chapter 5 - Seed source affects establishment and survival for three grassland species sown into reciprocal common gardens<sup>4</sup>

### Abstract

The source of plant material can affect the successful establishment and subsequent survival of plant species in restoration. Sometimes a local advantage is assumed or advocated, but research to date is equivocal on the relative success of local versus non-local plant sources in restoration. Global change, which is altering environmental conditions broadly and within local sites, raises additional questions regarding whether local sources will consistently perform best in the future. We investigated the effects of seed source (local vs. non-local) on the performance of three grassland species across variable environments using reciprocal common gardens in three states (Nebraska, Kansas, and Oklahoma). In order to mimic the restoration of grassland vegetation from seed under realistic conditions where species interact with one-another during establishment, we focused on three species (*Elymus canadensis*, *Oligoneuron rigidum*, and *Sorghastrum nutans*) that were seeded together into communities with nine additional grassland species, simultaneously and identically manipulating source for all species. Both common garden site and seed source affected initial (first year) establishment in terms of density and survival, but responses differed among seed sources and were not consistent among species. No seed source, including local, had a consistent advantage. Effects of seed source on initial density, in addition to survival, suggest that experiments utilizing transplants might miss important effects of seed source on establishment and that the relative performance of different sources within a single site or that of any one species across sites cannot be easily generalized.

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<sup>4</sup> Daniel Carter retains copyright. Chapter 4 is published in the open access journal *Ecosphere*: D.L. Carter & J.M. Blair, 2012. *Ecosphere*, 3(11):art102. <http://dx.doi.org/10.1890/ES12-00223.1>

## Introduction

While there is broad agreement that the source of plant material used in restoration projects matters, the basis for recommendations regarding local vs. non-local sources is often unclear. Common garden experiments can provide data on differences among source populations, and such experiments have shown that a broad range of plant traits or performance measures vary intraspecifically in many plant taxa according to provenance (e.g., Clauson et al. 1940, Linhart and Grant 1996, Leimu and Fischer 2008, Miller et al. 2011, Weißhuhn et al. 2011). Such intraspecific variation is typically explained by spatially heterogeneous selective forces acting on trait variation to tune populations to local environmental conditions, although other factors (e.g., gene flow) can also influence local differentiation among plant populations (Kawecki and Ebert 2004). In many cases, evidence of neutral genetic variation among sites is used as a proxy for local adaptation (e.g., Gustafson et al. 2004, Selbo and Snow 2005, Moncada et al. 2007). The assumption that observed trait or genetic differences among source populations are important often forms the basis for recommending the use of locally sourced plant material (Hamilton 2001, Miller et al. 2011), as do concerns regarding the loss of local genetic diversity with the introduction of new genotypes (Keller et al. 2000, Wilkinson 2001, Hufford and Mazer 2003). However, relatively few studies have shown that survival or demographic rates differ among sources or between local and non-local sites (e.g., Souther and McGraw 2011, Van der Veken et al. 2012). There are also few studies to indicate whether any intraspecific differences observed among sources grown in single common gardens are consistent across multiple sites or among co-occurring species (e.g., Waser and Price 1985, Bischoff et al. 2006). Further, most common garden studies grow plants in isolation from interspecific interactions (e.g., Miller et al. 2011), but the presence of other species can affect the magnitude of source effects for focal species (Bischoff et al. 2006, Rice and Knapp 2008). In reality the restoration of focal plant

populations often occurs in the presence of other species, and many restoration projects involve the introduction of seeds or transplants representing several or many species to areas where native vegetation has been mostly or completely removed (e.g., Cottam and Wilson 1966, Middleton et al. 2010, Carter and Blair 2012). Despite this, we are not aware of any studies to date that simultaneously manipulate source for more than two species concurrently, though Genung et al. (2012) manipulated source for two species.

The relative advantages of using local vs. non-local sources may be further complicated as a result of changing environmental conditions. Global change is likely to affect the suitability of even local sources for contemporary and future environments (Broadhurst et al. 2008). Landscape fragmentation has reduced many populations to small, isolated relicts, which may possess reduced genetic diversity (Ellstrand and Elam 1993, Keller and Waller 2002). Anthropogenic climate change (Strzepek et al. 2010, Rahmstorf and Coumou 2011), nutrient deposition (Galloway et al. 2004), increases in atmospheric CO<sub>2</sub> (Hansen et al. 1981, O'ishi et al. 2009), and the near ubiquitous presence of introduced producers and consumers (Walther et al. 2009, Burgiel and Muir 2010) are causing worldwide shifts from historical environments. Recognition of the many potential effects of multi-dimensional global change has increased debate regarding managed relocation (e.g., McDonald-Madden et al. 2011) and management for desirable characteristics in novel ecosystems (Seastedt et al. 2008).

Harris et al. (2006) call for the use of common garden experiments as “proactive research and action” in the context of global change, because common gardens elucidate the responses of organisms to environmental variation. Multiple common garden sites can provide insights into the relative success of different sources of plant material under a range of environmental conditions. In this study, we assessed the effects of seed source on the initial

establishment of species commonly used in tallgrass prairie restoration across three common garden sites in the Central United States. Rather than grow plants in isolation or monoculture, we sowed twelve species into restoration plots in combination and manipulated seed source for all species identically and simultaneously. We tracked establishment and survival over one year for three species (see Methods). Direct sowing of seeds into common gardens avoids any potential for artificial selection for plants that germinate and survive in the greenhouse prior to transplant into the field. It also provides the additional advantage of recreating a common grassland restoration approach where multiple species are sown and allowed to establish simultaneously. In this study, our focal species grew in the context of interspecific interactions, so interpretation of differences among sources within sites, or among sites sown with the same source, varies slightly from common garden experiments using a single species (e.g., Miller et al. 2011). In this context, observed differences reflect a combination of the direct effects of common garden site environments on the focal species as well indirect effects of site mediated through site effects on the other sown species. Our overarching goal was to assess the effects of seed source and environmental variation on the establishment of three common tallgrass prairie plant species where multiple species co-occur. Specifically, we ask (1) do plants exhibit greater survival or populations exhibit greater establishment densities when they are derived from a particular source? (2) Are any observed differences in survival or establishment density among sources consistent among sites, or is there a source by site interaction? (3) Do the three species exhibit qualitatively similar responses to seed source and common garden sites (i.e., how generalizable are the responses?)? Initial establishment in a restoration is important not only for the creation of viable populations of sown species, but also because early pre-emption of space should enhance priority effects of target vegetation against weeds (e.g., Sutherland 1974). Similar responses

among the three species, which belong to different functional groups, would increase confidence that responses can be more broadly generalized in tallgrass prairie restoration.

## **Methods**

### ***Species selection and reciprocal common gardens***

We chose twelve species that occur commonly on native grasslands near all sites and for which viable seeds were produced and collected in 2009. Seed mixtures contained warm-season grasses and composite forb and legume species that respectively contribute the most to dominance and diversity in Central North American grasslands (Howe 1994, Towne 2002). We collected seeds for all species from native prairies near (all within 100 km) each common garden site and stored them in paper bags at 20–24°C for between 0.5 and 5 months (depending on when seeds matured for different species at different sites). We tested seeds for viability (tetrazolium test) at the Kansas Crop Improvement Association seed laboratory to permit the sowing of equal weights of live seeds for each species within each mixture to each treatment plot.

Seeds from the twelve native, grassland species were hand broadcast into ex-arable plots in Nebraska (NE), Kansas (KS), and Oklahoma (OK) in late December, 2009, and early January, 2010 (see Appendix C for site characteristics). These sites were chosen to cover a broad range of regional climatic conditions, and because they had areas dedicated to research (especially NE and KS), other restoration activities were already occurring at the sites, there were agricultural fields available to be restored, and there were locally available native grasslands to serve as seed sources. Plots were 9 × 9 m with 0.5 m buffers for each of three seed source treatments and arranged in a randomized complete block design at each site (12 total plots/site × 3 sites: NE, KS, and OK sources). To ensure uniform dispersal of species within plots, seed additions for all treatments contained equal live weights for each of the twelve added grassland species (see

Appendix C for sowing details). We assumed that effects of seed banks and dispersal from adjacent sites were minimal for sown species (all perennial) due to crop production at all sites immediately prior to seed addition. The nearest populations for all species were >20 m away from experimental plots. We chose three focal species from among the twelve for this study: *Elymus canadensis* (Canada wild rye, C<sub>3</sub> perennial grass), *Oligoneuron rigidum* (stiff goldenrod, C<sub>3</sub> perennial forb), and *Sorghastrum nutans* (indiangrass, C<sub>4</sub> perennial grass). We chose these species because they represent different functional groups, and they were initially abundant across source treatments and common garden sites.

### ***Sampling and populations measurements***

In both May (10–30) and August (10–30), 2010, we counted the number of stems for each species within six 0.25 m<sup>2</sup> quadrats placed randomly along each of four equidistant transects within each plot (6 × 4 subsamples/plot). Plot-level density for each of the focal species on each sampling occasion was determined as the average across all 24 quadrats within each plot. May densities reflect primarily initial emergence of seedlings. August densities integrate several processes, including any recruitment of seedlings after May sampling, mortality, and the production of additional stems by individual plants. We use August density as an index of initial establishment for each species, and the relative difference between May and August densities  $[(\text{Density}_{\text{August}} - \text{Density}_{\text{May}})/\text{Density}_{\text{May}}]$ , which is the intrinsic population growth rate ( $r$ ), as an index of population performance through the course of the first growing season. We also tracked the survival of individual plants for the three focal species between May and August, 2010. On each plot at each site we marked the first 25 seedlings of each of the three species encountered while performing May counts of stems (Fig. 5-1). In many cases, particularly at the OK site, we encountered fewer than 25 seedlings with this approach, so we searched the plots haphazardly



and added any additional seedlings we could find. We also added a few seedlings that we encountered for the first time in June. In several cases, more than 25 seedlings were marked on an individual plot, particularly when there was concern that other plots at a particular common garden site had < 25 seedlings. Regardless, we retained all plants we marked initially for analysis. We surveyed the plants again in August, and we assumed the plants had died, if no live tissue was present aboveground. Changes in  $r$  (May – August relative differences) inconsistent with patterns of survival for individual plants could result from either additional seedling recruitment or stem production by surviving plants.

### ***Data analysis***

We used generalized linear mixed models to test for differences in density and proportional survival for each of the three focal species with seed source treatment and common garden site as fixed effects and block within site as a random effect. We performed these analyses in SAS version 9.2 (2011, Cary, North Carolina, USA) using Proc Glimmix. For density, we used an identity link and Kenward-Roger degrees of freedom estimation. For the number of plants surviving in August/plants marked in May we used a logit link and Satterthwaite degrees of freedom estimation. Parameter estimates for survival are odds rather than mean proportions, although we present proportions for the sake of interpretability in Fig. 5-3.

## **Results**

### ***Density***

There were significant site effects and at least marginally significant source  $\times$  site effects on *E. canadensis* May stem density, August stem density, and  $r$ , but a significant source effect

occurred only for May stem density (Table 5-1). In both May and August, *E. canadensis* stem density was lower in OK than NE for all sources and lower in OK than KS for the NE source, and the OK source had lower density in cases where there were differences among sources within sites (Fig. 5-2A, B). Stem populations increased for all sources at the NE site,  $r$  was not significantly different from zero for all sources at the KS site and OK and KS sources at the OK site, and populations sourced from NE decreased at the OK site (Fig. 5-2C).

There were significant site effects on *O. rigidum* May stem density, August stem density, and  $r$ , but significant source and at least marginally significant source  $\times$  site effects occurred only for May and August stem densities (Table 5-1). In May, stem density of *O. rigidum* was higher at the NE site than KS and OK sites for the NE source (Fig. 5-2D), but by August stem density was greater for all sources at the NE site compared to the KS site and for two of three sources compared to the OK site (Fig. 5-2E). Stem populations increased at the NE site,  $r$  was not significantly different from zero at the KS site, and populations decreased at the OK site across seed source treatments (Fig. 5-2F).

There were significant site effects on *S. nutans* May stem density, August stem density, and  $r$ , significant source effects on May and August stem density, and a marginally significant source  $\times$  site effect on August stem density (Table 5-1). In May, the density of *S. nutans* stems across sources was greater at the NE than the OK and KS sites, and density was greater for the KS source than the OK source across sites (Fig. 5-2G). In August, stem densities at the NE site were greater than those at the KS and OK sites for all sources, and at both the NE and KS sites, the density was greater for the KS source than the OK source (Fig. 5-2H). Stem populations increased across source treatments at the NE and KS but not the OK site (Fig. 5-2I).

## *Survival*

There were no significant main effects of source on survival among the three species, but there were significant site effects on *E. canadensis* and *O. rigidum* survival, and a significant source  $\times$  site effect on *E. canadensis* survival (Table 5-2). The odds of survival for *E. canadensis* varied by site and by source within the KS and OK sites. The odds of survival were greater in NE than OK (Fig. 5-3A). In KS, the NE source had greater odds of survival than the OK source, and in OK, the OK source had greater odds of survival than the NE source (Fig. 5-3A). The odds of survival for *O. rigidum* varied by site, with greater odds of survival at the NE and KS sites compared to the OK site (Fig. 5-3B). There was no evidence for differential survival odds of *S. nutans* among sites or sources (Fig. 5-3C).

## **Discussion**

Biophysical filters on establishment can act on trait variation to modulate survival (Hobbs and Norton 2004). Patterns of early and late season density, density change ( $r$ ), and survival provide insights into the action of biophysical filters on the initial establishment of the focal species in our study. Already in May, differences in density for all three focal species existed between sites, and the three species also exhibited differences among sources within particular sites. Subsequently, stem populations increased, decreased, or remained static, with responses depending on common garden site, source, and species. These changes were consistent with differences in survival, which was generally lower in OK than in NE and KS (exceptions: *S. nutans* and the OK source of *E. canadensis*). The environmental difference among sites in our study was multivariate, and we will not attempt to identify particular causes for differences in density or survival for the focal species among sites or among sources within sites. Nonetheless, our results indicate that source can affect species establishment when species are grown in a

community setting that is comparable to a real restoration, but the identity of best-performing sources in terms of density and survival may differ by site and species.

Our results do not indicate a general local advantage in initial establishment for the focal species. Among all cases where the sources differed among or within sites (significant source or source  $\times$  site effect, respectively), the local source performed best in terms of a statistical difference in density or density change ( $r$ ) for one species at only one site (*O. rigidum* density in NE), and there were no cases where the local source significantly outperformed all others in terms of survival. In some cases, the best performing source within a site was not local (e.g., *E. canadensis* density in KS) or a particular source tended to perform well across the three sites (e.g., *S. nutans* density). Such equivocal results regarding local advantage are similar to those arrived at from other work (e.g., Bischoff et al. 2006), including a study of several species that often co-occur in natural communities (Weißhuhn et al. 2011). While source did not always affect survival, it did affect both May and August density for all species at all sites (source effect and/or source  $\times$  site interaction). For example, we did not find differences in survival among sources of *O. rigidum* or *S. nutans* through the growing season, but we observed differences among sources in the densities of plants that established from seed for all three species. Because seeds were sown on a unit weight per area basis, the densities we observed do not necessarily reflect germination rates. Still, we think this discrepancy is important, because it suggests that effects of source, or a lack thereof, based on studies using transplants (e.g., van der Veken et al. 2012) do not always parallel source effects on germination and emergence. This is of clear, practical, importance for restoration projects that depend upon seed inputs (e.g., Martin and Wilsey 2006). Delayed coverage of seeded vegetation in restoration could lead to the persistence

of weeds through priority effects (Sutherland 1974), which in turn could diminish the establishment of desired vegetation (Blumenthal et al. 2003).

Differential source relationships among sites within species are not surprising, as many environmental factors have the potential to interact to create conditions at sites that differ from historical conditions to which local sources may be matched (Broadhurst et al. 2008). Lack of generality in effects of seed source among species or site locations is unfortunate, because predictability is a desired characteristic of restoration projects (Benayas et al. 2009), and variable outcomes based on combinations of potential species, sources, and sites for projects present a seemingly intractable problem. Our results show that the initial establishment of individual species in a community setting varies among distant sites with variable environmental conditions. The general conclusion, that the effects of source and site on establishment of different species are idiosyncratic applies to both establishment density and seedling survival. However, effects of source and site on establishment density highlight the importance of measuring responses that integrate the seed to seedling transition, particularly where passive seed dispersal or active seeding are important components of restoration efforts. Other authors have discussed the merits of managed relocation of sources based on measurements of performance (McDonald-Madden et al. 2011). Our results from multiple species in reciprocal common gardens suggest a more complex picture, where the location or conditions for which sources are evaluated and the identities of focal species matter. Given the lack of generality in responses among species or sites, the mixing of multiple seed sources might be explored as a potential means of decreasing the chance of poor seedling survival or initial establishment for species across variable sites (Broadhurst et al. 2008).

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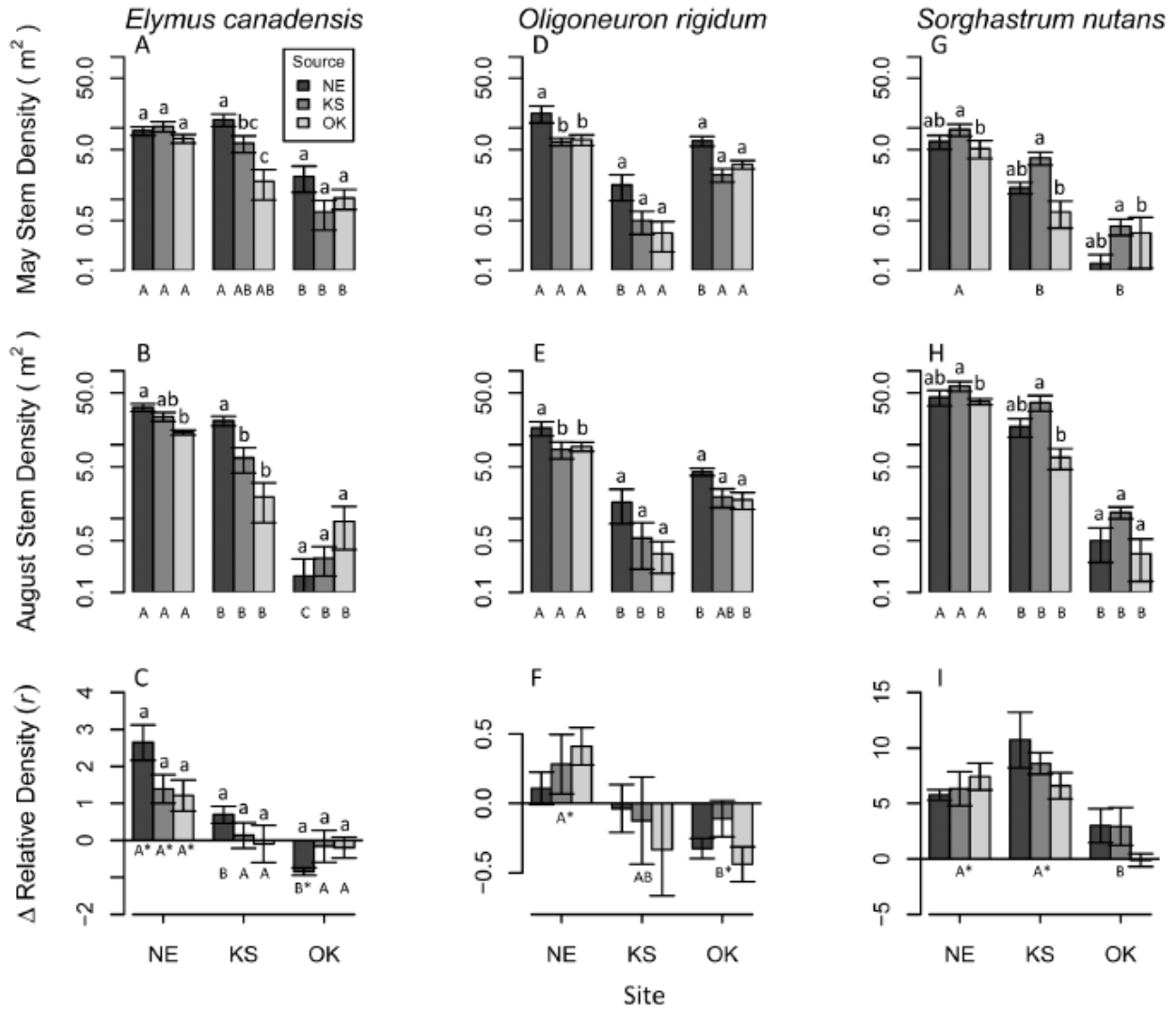
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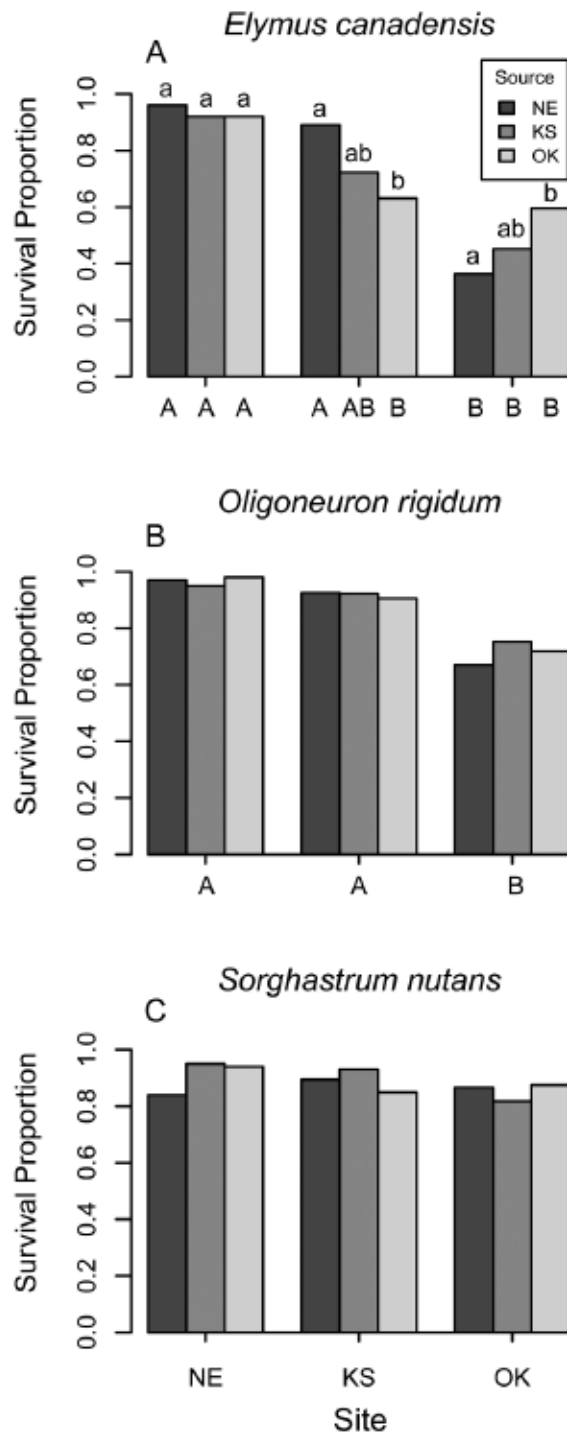
### Figures and Tables



**Figure 5-1.** Typical seedling (*O. rigidum*) marked in May to track survival through the growing season. The width of the nail head is 1.2 cm.



**Figure 5-2.** (A, D, G) May stem density, (B, E, H) August stem density, and (C, F, I), relative change (May–August) in stem density ( $r$ ) for *E. canadensis*, *O. rigidum*, and *S. nutans*  $\pm$  2 SE. Upper- and lower-case letters respectively indicate significant differences among sites and sources (or among sites within sources and sources within sites if interaction  $p < 0.1$ ) (Table 5-1) after alpha adjustment (adjust = simulate, SAS). Asterisks indicate significant differences from zero for source 3 site combinations (C) or sites (F, I).



**Figure 5-3.** Proportional survival for (A) *E. canadensis*, (B) *O. rigidum*, and (C) *S. nutans* by seed source and common garden site. Upper- and lower-case letters follow Fig. 1. See Table 5-2 for main effects and interaction statistics

**Table 5-1.** Statistics for source, site, and source×site effects on May stem density, August stem density, and  $\Delta$  relative density ( $r$ ) by species (Figure 5-1).

Species	Site		Source		Source × Site	
	F <sub>df</sub>	p	F <sub>df</sub>	p	F <sub>df</sub>	p
<i>Elymus canadensis</i>						
—May Stem Density	F <sub>2,27</sub> =26.29, p<0.001		F <sub>2,27</sub> =9.44, p<0.001		F <sub>4,27</sub> =5.18, p=0.00	
—August Stem Density	F <sub>2,27</sub> =79.67, p<0.001		F <sub>2,18</sub> =1.72, p=0.201		F <sub>4,18</sub> =2.75, p=0.061	
— $\Delta$ Relative Density	F <sub>2,9</sub> =22.46, p<0.001		F <sub>2,18</sub> =1.72, p=0.201		F <sub>4,18</sub> =2.75, p=0.061	
<i>Oligoneuron rigidum</i>						
—May Stem Density	F <sub>2,27</sub> =17.25, p<0.001		F <sub>2,27</sub> =12.12, p<0.001		F <sub>4,27</sub> =3.09, p=0.042	
—August Stem Density	F <sub>2,9</sub> =23.82, p<0.001		F <sub>2,18</sub> =9.40, p=0.002		F <sub>4,18</sub> =2.67, p=0.066	
— $\Delta$ Relative Density	F <sub>2,9.29</sub> =6.91, p=0.015		F <sub>2,17.89</sub> =0.43, p=0.656		F <sub>4,17.86</sub> =0.86, p=0.508	
<i>Sorghastrum nutans</i>						
—May Stem Density	F <sub>2,27</sub> =40.71, p<0.001		F <sub>2,27</sub> =5.65, p<0.009		F <sub>4,27</sub> =1.36, p=0.274	
—August Stem Density	F <sub>2,9.25</sub> =27.96, p<0.001		F <sub>2,17.57</sub> =10.10, p=0.001		F <sub>4,17.55</sub> =2.31, p=0.098	
— $\Delta$ Relative Density	F <sub>2,9.84</sub> =10.77, p=0.004		F <sub>2,16.26</sub> =1.56, p=0.239		F <sub>4,16.22</sub> =1.66, p=0.208	

Note: Statistics are F-statistic<sub>num. df,den. df</sub>, p-value (identity link, Proc Glimmix, SAS).

**Table 5-2.** Statistics for source, site, and source×site effects on seedling survival by species (Figure 5-3).

Species	Site		Source		Source × Site	
	F <sub>df</sub>	p	F <sub>df</sub>	p	F <sub>df</sub>	p
<i>Elymus canadensis</i>	F <sub>2,9</sub>	20.83, p<0.001	F <sub>2,27</sub>	2.55, p=0.097	F <sub>4,27</sub>	3.28, p=0.026
<i>Oligoneuron rigidum</i>	F <sub>2,6</sub>	8.5=11.75, p=0.006	F <sub>2,27</sub>	0.28, p=0.757	F <sub>4,27</sub>	0.88, p=0.487
<i>Sorghastrum nutans</i>	F <sub>2,9</sub>	8.4=3.02, p=0.095	F <sub>2,25</sub>	2.45, p=0.107	F <sub>4,25</sub>	1.31, p=0.292

Note: Statistics are F-statistic<sub>num. df,den. df</sub>, p-value (logit link, Proc Glimmix, SAS).

## **Chapter 6 - Seed source has variable effects on community and ecosystem properties of grassland restorations sown into reciprocal common gardens**

### **Abstract**

Research to date has produced equivocal results regarding the relative advantages of local versus non-local sources of plant material for restoration. This research has typically been based on assessing the performance of individual species at individual locations and without addressing higher order community and ecosystem properties. We investigated the effects of seed source (local, non-local, and mixed-source treatments) on species, community, and ecosystem properties across variable environments using reciprocal common gardens in three states (Nebraska, Kansas, and Oklahoma). In order to mimic the restoration of grassland vegetation under realistic conditions where species interact with one another during establishment, we seeded twelve species together between December, 2009 and January, 2010 and assessed responses in 2010, 2011, and 2012. Both common garden location and seed source affected the productivity of individual species, but responses were not consistent among species. No seed source had a consistent advantage across sites or across species. In a few cases, the local source was most productive for a particular species at one location, but no species showed a consistent local advantage across locations or years. Rather, in two out of three species that exhibited a local advantage at one location, the same source was also the most productive at a non-local site. Community structure and species richness differed among locations in all years, but source did not significantly affect seeded species richness, and source significantly affected community structure only in 2011. Despite source effects on individual species and community structure,



seed source had no significant effects on the combined productivity of seeded species. These results do not support the targeted use of local sources when the establishment of sown species (seeded species richness) and productivity are restoration objectives. Using mixed-source species mixtures may increase chances of restoration success, given the idiosyncrasy of individual species' responses among locations and potential site-specific environmental changes likely to occur in the future.

## **Introduction**

Phenotypes and genotypes of plant species vary across spatial and environmental gradients (Weißhuhn et al. 2011, Moncada et al. 2007, Gustafson et al. 2004). Such differences sometimes form the basis for recommending the use of locally sourced plant material when establishing, or restoring, native plant communities (Miller et al. 2011, Hamilton 2001), as do concerns regarding the loss of local genetic diversity with the introduction of new genotypes (Hufford & Mazer 2003, Wilkinson 2001). However, the presence or direction of source effects can vary among species (Carter & Blair 2012, Miller et al. 2011, Rice & Knapp 2008), and there is little empirical support to date for the assumption that local sources provide a competitive advantage or enhanced restoration outcomes.

Variable and changing environmental conditions can also affect the relative success of different plant sources. However, projected and realized changes in abiotic and biotic environments are seldom considered when assessing the advantages of local ecotypes. This may be increasingly important, as anthropogenic climate change (Rahmstorf & Coumou 2011, Strzepek et al. 2010), nutrient deposition (Galloway et al. 2004), increases in atmospheric CO<sub>2</sub> (O'ishi et al. 2009, Hansen et al. 1981), and the presence of introduced producers and consumers (Burgiel & Muir 2010, Walther et al. 2009) continue to cause worldwide shifts from historical

environments. Recognition of the many potential effects of such changes has increased debate regarding managed relocation, for example (e.g. McDonald-Madden et al. 2011). Seastedt (2008) also emphasizes that global change may necessitate management towards novel rather than historic communities, if the management goal is ecosystem stability and function. Further, landscape fragmentation has reduced many populations to small, isolated relicts, which may possess reduced genetic diversity (Keller & Waller 2002, Ellstrand & Elam 1993). This makes it more likely that low genetic variation may limit their evolutionary potential to meet environmental challenges (Broadhurst et al. 2008), although these effects should be expected to vary among species with different traits (e.g. pollination syndromes) or whose populations are structured at different spatial scales (Loveless et al. 1984). Where genetic variation is limited, increasing or changing available variation may improve or change responses to natural selection (Rice and Emery 2003). Broadhurst et al. (2008) and Harris et al. (2006) ask whether the exclusive use of local material limits the ability of restoration projects to adapt to predicted climate change, and Harris et al. (2006) call for the use of common garden experiments as “proactive research and action” in the context of global change. In particular, multiple common garden sites can provide insights into the relative success of different sources of plant material under a range of environmental conditions.

In this study, we used three common garden locations in the U.S. Central Plains to assess the effects of different seed sources (local, non-local and mixed) on the productivity of individual species growing in mixed species communities, species richness and community structure, and the combined aboveground productivity of all seeded species. These common gardens were established in the context of tallgrass prairie restorations, using native grassland species common to all sites. Our experimental approach (common gardens at multiple locations

with simultaneous source manipulation of multiple species) was motivated by the fact that few common garden studies to date have assessed whether any intraspecific differences observed among sources are consistent across multiple locations or among co-occurring species (e.g. Bischoff et al. 2006, Waser & Price 1985). Most common garden studies also have grown plant species in isolation, precluding any effects of interspecific interactions (e.g. Miller et al. 2011). However, the presence of other species can affect the magnitude of source effects for focal species (Rice & Knapp 2008, Bischoff et al. 2006). In reality the restoration of focal plant populations often occurs in the presence of other species, and most restoration projects involve the introduction of native vegetation representing several or many species (e.g. Middleton et al. 2010, Cottam & Wilson 1966). Despite this, we are unaware of any prior studies that simultaneously manipulated sources of multiple species and then evaluated species, community, and ecosystem responses concurrently. Filling this gap in knowledge is important, because individual species and/or community properties (e.g. richness or dominance) can affect productivity (Isbell et al. 2011, Fornara & Tilman 2009, Smith et al. 2003, Huston 1997). Figure 6-1 presents a framework illustrating how single species responses might affect community and ecosystem properties (e.g. productivity). Source effects that are homogenous among species (circles) may affect productivity. However, productivity may also vary if source effects exist but exhibit different patterns among species, leading to differences in community structure.

We established common gardens of tallgrass prairie restorations in Kansas (KS), Nebraska (NE), and Oklahoma (OK), using seed sources from each location in each of the common garden sites. Each common garden included plots with local sources only, non-local sources from two other sites, and a mix of local and non-local sources. Our framework allowed us to ask: 1) Are there seed source effects on the productivity of individual seeded species when

they are grown in the context of plant communities? 2) Does seed source affect community properties such as structure or richness? 3) Does seed source affect the combined productivity of seeded species? Both productivity and richness are common measures of restoration success (Guo 2007, Ehrenfeld 2001). In addition, we implemented a treatment within each common garden where multiple seed sources were mixed together. We predicted that because this mixed treatment contains at least some variation from each of the locations for each species, that it should not underperform in terms of total productivity or that of its constituent seeded species relative to other treatments (Broadhurst et al. 2008).

## **Methods**

### ***Species selection and reciprocal common gardens***

We chose twelve species that occur commonly in native grasslands near all three locations where common gardens were established. We identified many more species that occurred in grasslands near all locations, but the twelve species we chose represent the subset of species that were both common and that produced adequate amounts of viable seed in 2009. These included warm-season grasses and composite forb and legume species, groups that respectively contribute the most to dominance and diversity in Central North American grasslands (Howe 1994, Towne 2002). We collected seeds from native prairies near each common garden location and stored seeds in paper bags at 20-24 °C for between 0.5 and 5 months. We tested seeds for viability (tetrazolium test) at the Kansas Crop Improvement Association seed laboratory to permit the sowing of equal weights of live seeds for each species within each mixture to each treatment plot.

Seeds were hand broadcast into ex-arable plots at locations in Nebraska (NE), Kansas (KS), and Oklahoma (OK) in late December, 2009, and early January, 2010. These locations

were chosen to cover a broad range of regional abiotic conditions. In particular, long term average temperature and precipitation, observed precipitation during this study, and soil texture varied among locations (See Appendix C for details).

Plots were  $9 \times 9$  m with 0.5 m buffers for each of four seed source treatments and arranged in a randomized complete block design at each location (16 total plots/location  $\times$  3 locations). Treatments included seed sourced from single locations (3 treatments; NE, KS, and OK) and a treatment that mixed seed from the three sources in equal proportions. To ensure uniform dispersal of species within plots, seed additions for all treatments contained equal live weights for each of the twelve added grassland species (see Appendix C for sowing details). We assumed that seed banks and dispersal from adjacent locations had minimal effects for sown species (all perennial). This assumption is supported by histories of crop production at all locations immediately prior to seed addition and because nearest populations for all species were  $> 20$  m away from plots at each location.

### *Sampling*

We used accumulated aboveground biomass at the end of the growing season as an index of aboveground net primary productivity (ANPP). Biomass was harvested to within 1 cm of the soil surface in September 4-18, 2010, September 18-26, 2011, and August 18-26, 2012. Harvests were timed to occur at or near peak standing crop. In 2010, we harvested aboveground biomass from within each of six  $0.25 \text{ m}^2$  quadrats placed randomly within each plot (6 subsamples/plot) at each common garden location and sorted it by seeded and adventitious species. Seeded biomass was not sorted by individual species in 2010. These methods were repeated in 2011 and 2012, but we additionally sorted seeded biomass by individual seeded species. Due to a wildfire in 2011 biomass could not be collected at the OK location. The OK location was not sampled in

2012 either, because seeded species were nearly absent from the location (~1-2 plants / treatment plot), possibly due to severe drought. All samples were stored in paper bags for no more than one day prior to being dried for 48-72 hours at 60 °C. We measured seeded species richness at all three locations in 2010 and 2011 and in KS and NE in 2012 as the total number of species observed from May and August censuses of 24 randomly placed 0.25 m<sup>2</sup> quadrats (area 6 m<sup>2</sup>) in each plot (plot area 9 m<sup>2</sup>).

### *Data analysis*

We used separate generalized linear mixed models in each year to test for differences in biomass for each of the four most productive species, total seeded biomass, and species richness. Seed source treatment and common garden location were fixed effects and block within location was as a random effect. We performed these analyses in SAS ® version 9.2 (2012, Cary N.C.) using Proc Mixed with Kenward-Roger degrees of freedom estimation. In cases of unequal variances among locations, we used the local=exp(trt) option within the REPEATED statement to model unequal variances and Satterthwaite degrees of freedom estimation. Family-wise error rates were controlled for pairwise contrasts using the Tukey-Kramer alpha adjustment in the lsmeans statement (adjust=Tukey).

Community structure analyses were executed within the VEGAN package (Oksanen et al. 2012) using Program R version 2.14.2 (R Core Team 2012). Separate analyses were performed for the second (2011) and third (2012) growing seasons. We used non-metric multidimensional (NMDS) scaling with Ružička (quantitative Jaccard) dissimilarity matrices based on biomass (all seeded species) to visualize differences in seed community structure between NE and KS locations and among seed source treatments using function “metaMDS”. We assessed significance of source, location, and their interaction for explaining community structure using

permutational multivariate analysis of variance on Ružička distance matrices executed with function “adonis”. In cases of significant location  $\times$  source interaction, we tested effects of source within individual locations. Ružička dissimilarity is based on relative abundance (biomass) rather than presence/absence data, so analyses represent community structure rather than composition.

## Results

### *Species*

In order, the four most abundant species in terms of biomass across years and locations were *Sorghastrum nutans*, *Oligoneuron rigidum*, *Achillea millefolium*, and *Elymus canadensis* (hereafter referred to by genus). We focus on biomass patterns for these species (representing 92.4% of total seeded species biomass across locations and years), but biomass and associated statistics for less abundant species are presented in Appendix C. Source effects differed among locations, species, and years (Fig. 6-2).

Seed source effects on *Sorghastrum* biomass differed between locations in both years, and the KS source was consistently among the most productive (Fig. 6-2a-b). The OK source was more productive than the NE source at the NE location in both years (Fig. 6-2a-b), but the NE source was more productive than the OK source at the KS location in 2012 (Fig. 6-2b). The mixed source treatment was not the most productive at either location in either year, but it was as productive as at least one other treatment (Fig. 6-2a-b).

Productivity was greatest at the NE location for *Oligoneuron* in both years (Fig. 6-2c-d). In 2011, the NE source was more productive than the KS and OK sources at the NE location (Fig. 6-2c), but there were not differences among source treatments in 2012 (Fig. 6-2d). In both

years the mixed source did not differ significantly in productivity from the most productive and least productive source treatments at both locations (Fig. 6-2c-d).

Productivity for *Achillea* was greatest at the NE location in 2011 and greatest at the KS location in 2012 (Fig. 6-2e-f). There were no seed source effects on *Achillea* productivity (Fig. 6-2e-f).

Seed source affected *Elymus* productivity similarly at the NE and KS locations in 2011, but there was no evidence for seed source effects in 2012 (Fig. 6-2g-h). The NE source was consistently among the most productive at the KS and NE locations in 2011 (Fig. 6-2g), and the mixed source did not differ significantly in productivity from the most productive and least productive source treatments across locations and years (Fig. 6-2g-h).

### ***Community properties***

Species richness differed among locations in each year, but there were no significant effects of seed source on species richness (Fig. 6-3). Community structure differed among locations in 2011 and 2012 and differed among sources in 2011, but source differences in community structure were not consistent between NE and KS common garden locations (Fig. 6-4, Adonis within locations: source<sub>NE</sub>;  $F_{3,15} = 2.25$ ,  $p = 0.005$ , source<sub>KS</sub>;  $F_{3,15} = 1.95$ ,  $p = 0.006$ ).

### ***Productivity (ANPP)***

The total aboveground productivity of combined seeded species differed among locations in 2010 and 2011 with greater productivity at the NE location (Fig. 6-5a, b). However, seeded productivity was not significantly different between the KS and NE locations in 2012 (Fig. 6-5c). Seeded productivity did not significantly differ among source treatments in any year (Fig. 6-5).



## Discussion

Our results do not indicate a general local advantage in terms of aboveground productivity of individual species or the total community. Although there were some significant source effects in the productivity of individual species, where the local source for a particular species at a particular location performed best, the same source also performed well where it was not local (e.g. *Sorghastrum* sourced from KS, *Elymus* sourced from NE). The presence of source effects or the identity of the source that performed best also differed among species. Such equivocal or idiosyncratic results regarding local advantage for different species are not unique (e.g. Weißhuhn et al. 2011, Bischoff et al. 2006), suggesting that the assumption of local source superiority is not well supported by empirical data. One potential reason is that local environments can experience high variability in environmental conditions, which may alter the advantages of different ecotypes. For example, conditions in KS and OK were drier than average throughout this study, while conditions in NE were wetter than average in 2011 and drier than average in 2012 (Appendix C). In addition, the contemporary environments of many sites may not reflect past conditions due to prior agricultural use (Tiessen et al. 1982) and larger scale environmental changes (e.g. Galloway 2004, Hansen 1981). Such changes have the potential to interact to create conditions that differ from historical conditions to which local sources may be matched (Broadhurst et al. 2008), which could influence source effects. Source effects were more pronounced among the most abundant species in 2011 than 2012, which may explain why we detected seed source effects on community structure in 2011 (Fig. 6-1a) but not 2012 (Fig. 6-1a,c). Productivity may not have significantly differed among sources, even in 2011 when community structure differed, because sources did not differ in terms seeded species richness (Isbell 2011). This may have maintained the possibility that a species with relatively high productivity could compensate for another with lower productivity (e.g. Yachi & Loreau 1999).

Differences in environmental conditions may explain effects of site location on individual sown species and their combined productivity. Soil texture, and observed temperature and precipitation varied across common garden locations (see Appendix C). The productivity of C<sub>4</sub> grasses in Central Plains grasslands is positively associated with precipitation and sand, but the productivity of C<sub>3</sub> grasses is negatively associated with soil sand content (Epstein et al. 1997a), and varies with temperature when precipitation effects are accounted for (Epstein et al. 1997b). Here, identical seed mixtures resulted in different community structures at different locations, which suggests that location environmental differences were important determinants of community structure (e.g. Myers & Harms 2011, Tilman 1997). Differences in productivity among common garden locations may also result from differences in communities, as well as differences in the performance of individual species (e.g. Kahmen et al. 2005).

The lack of generality in effects of seed source on single species is consistent with our prior work that focused on the initial establishment and survival of *Sorghastrum*, *Oligoneuron*, and *Elymus* within this experiment (Carter & Blair 2012). These patterns are unfortunate when viewed in terms of idiosyncratic and variable patterns of source effects among individual species, because predictability is a desired characteristic of restoration projects (Benayas et al. 2009). However, seed source may be less important for higher order properties like productivity, because source effects on combined productivity need not mirror source effects on the productivity of single species (Fig. 6-1b). Tilman (1996) showed that instability in productivity within species could contribute to the stability of productivity among species.

While mixtures of the three sources did not significantly outperform single source treatments in terms of combined productivity or the productivity of individual species, mixtures also never performed significantly worse than the least productive single source treatment. Given

the lack of consistent source responses among species or locations, the mixing of multiple seed sources may deserve further exploration as a potential means of decreasing the chance of low single species or combined productivity across variable locations (e.g. Broadhurst et al. 2008).

Had we used single species in a single common garden in a single year, or had we investigated many species in isolation from interspecific interactions, we may have found support for local advantage. In 2011, three of eight, and in 2012, one of eight single species responses would have suggested that local sources are best (Fig. 6-2). Conversely, we may have found no source effects at all. While we utilized only a subset of the potential diversity in tallgrass prairie systems, our results strongly suggest that investigations of source effects on single species, particularly if narrow in spatial or temporal scope, have the potential to misinform the management or restoration of natural systems.

Our results from multiple species grown in the more realistic context of interspecific interactions do not support the targeted utilization of local sources in restoration. Natural selection may still act, or have acted in the past, to tune source populations to their local environments (Linhard & Grant 1996). However environmental changes and potential losses of genetic diversity (see Introduction) may lead to changes in the relative performance of sources at particular locations and may affect whether or not the raw genetic material is present for selection in the first place. Managed relocation based on performance measures as an alternative approach to relying on local sources for restoration and conservation may address such mismatches between genes and environments (McDonald-Madden et al. 2011). However, our research suggests that unique species responses will likely make that approach less tractable when the restoration of communities is an objective. We may safely bet that environmental changes will continue, but there is more uncertainty surrounding the prediction of local than

global change (Kerr 2011). Using mixed-source species mixtures, which did not perform significantly worse than exclusively locally-sourced species mixtures under present conditions, may represent an alternative way of hedging bets in a changing world.

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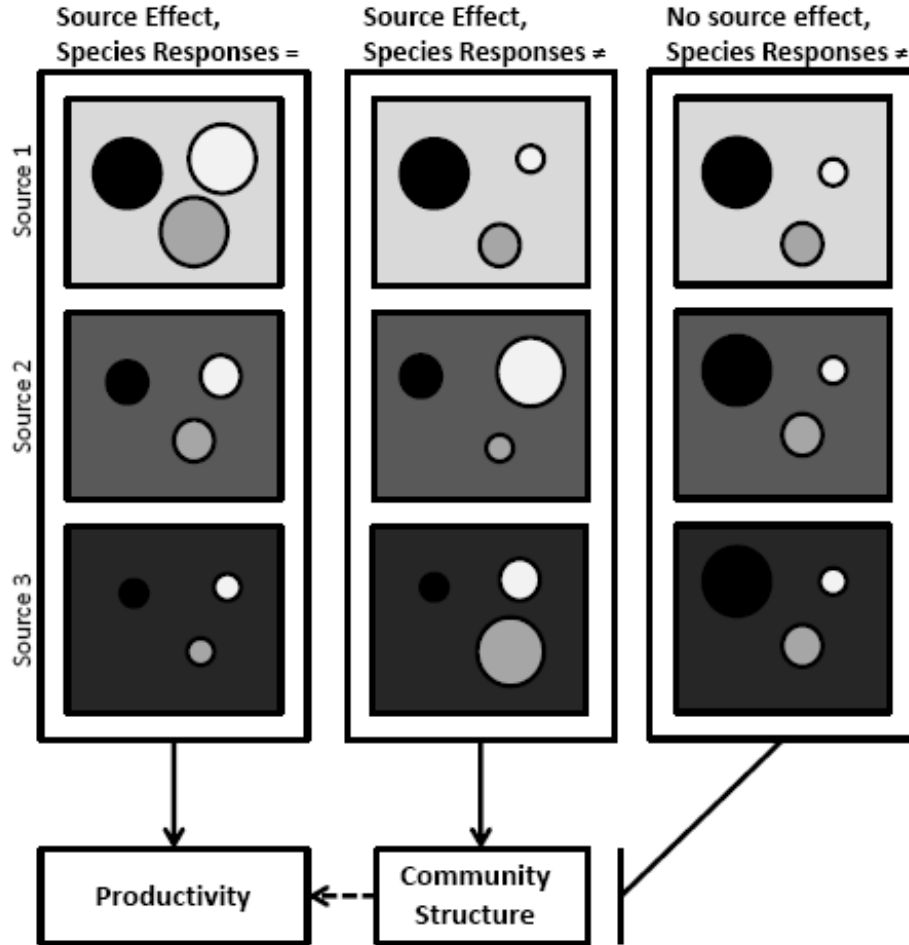
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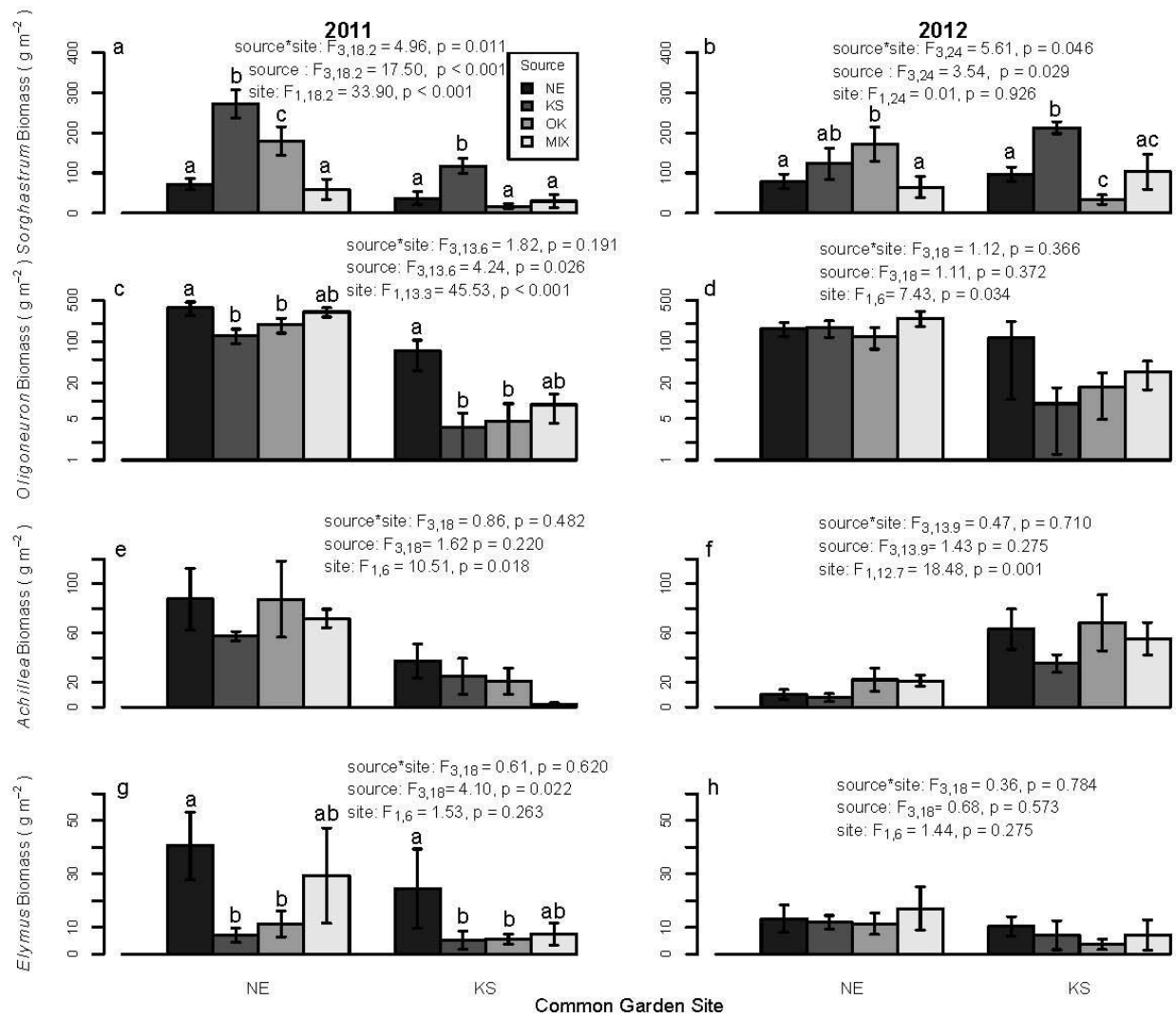
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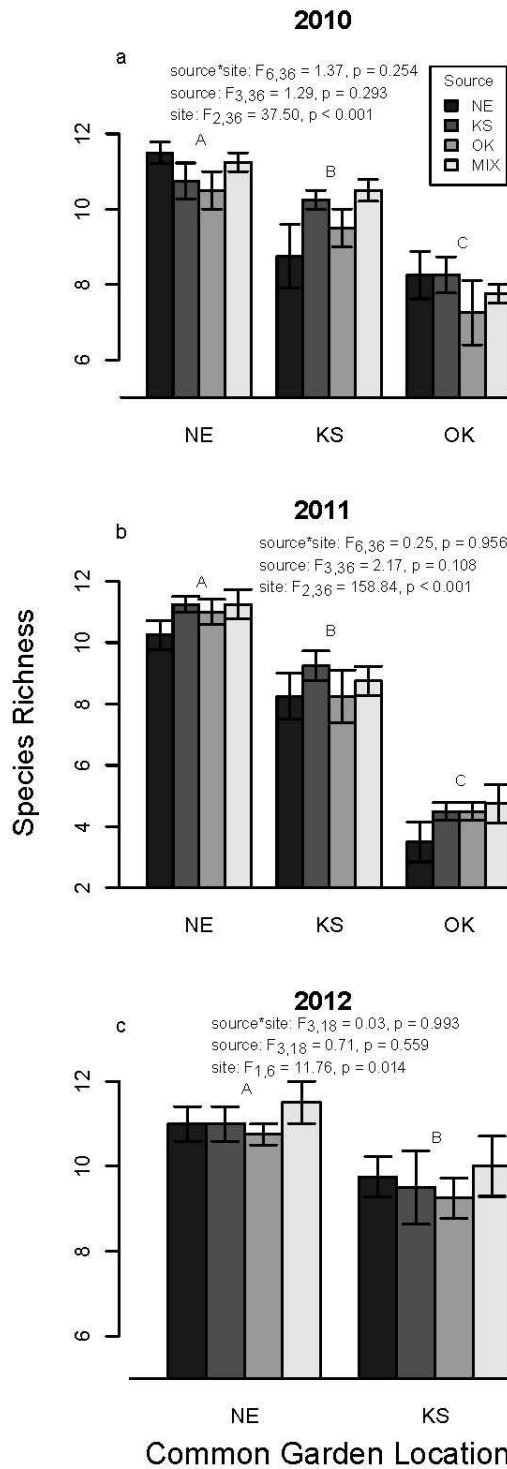
## Figures and Tables



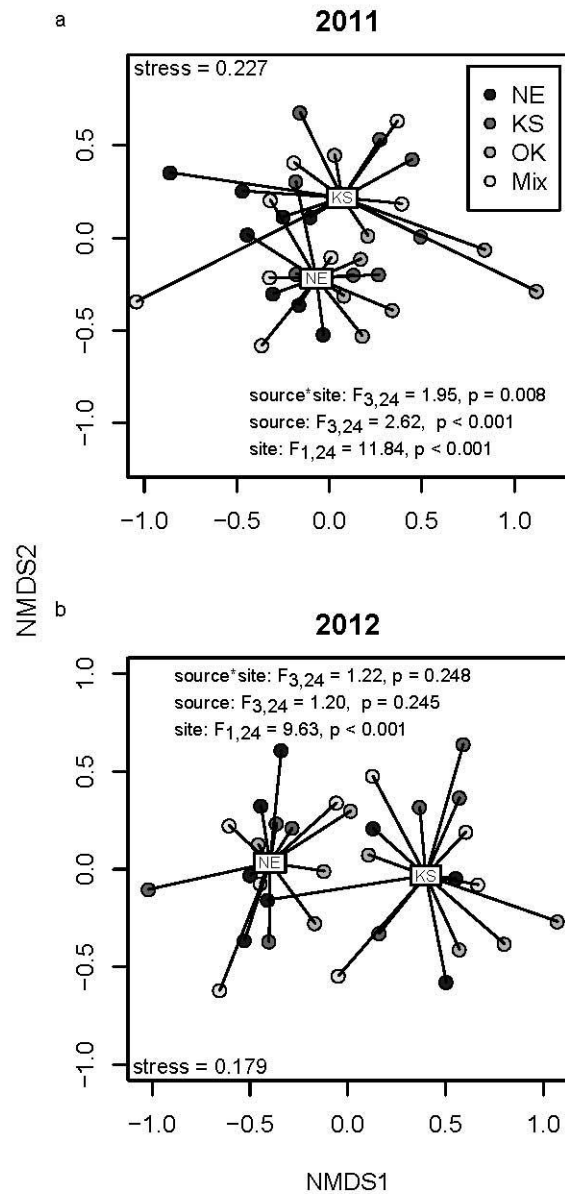
**Figure 6-1.** Conceptual framework showing how individual species responses might affect productivity at one location (common garden). Solid arrows indicate effects, the dashed arrow represents potential effects, and intersecting solid lines indicate no effect. In the first column, similar species responses to seed source cumulatively affect productivity. In the second column, differential species responses to seed source affect community structure, which may or may not affect productivity depending on the substitutability of responses. In the third column, species responses differ homogenously among sources, leading to similar community structures.



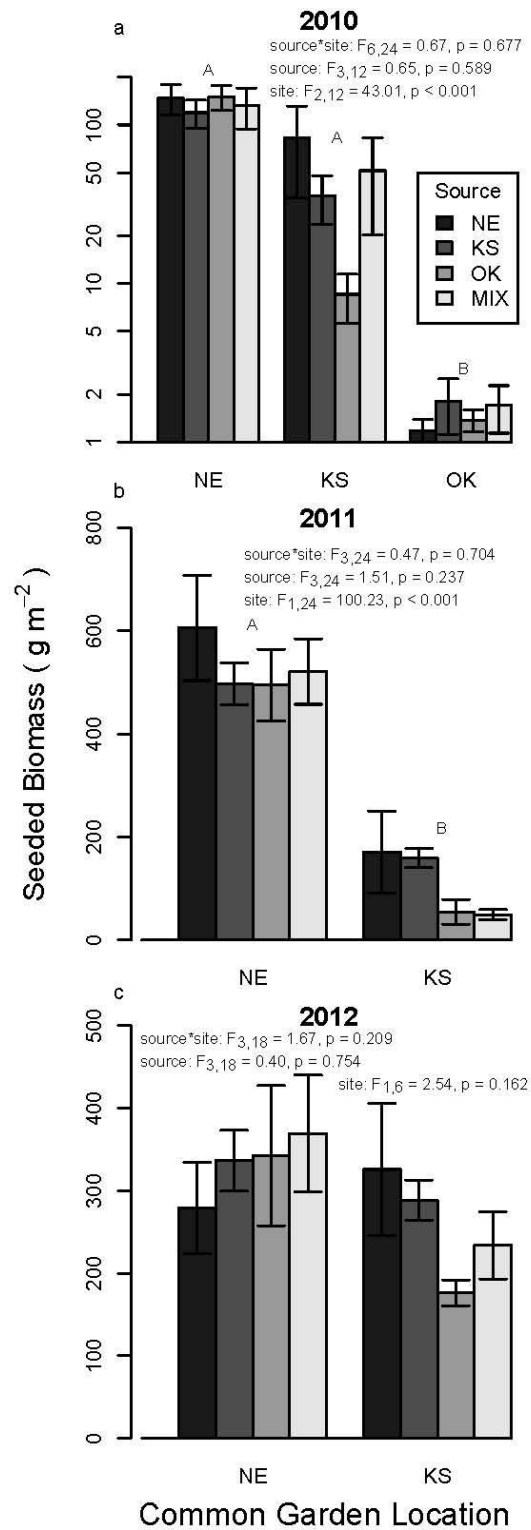
**Figure 6-2.** Aboveground biomass from 2011 (a, c, e, g) and from 2012 (b, d, f, h) for the four most abundant species across years and common garden locations *Sorghastrum*, *Oligoneuron*, *Achillea*, and *Elymus* (mean  $\pm$  1 s.e.m.). Lower-case letters indicate significant differences among sources within locations (interaction  $p \leq 0.05$ ) or among sources across locations (interaction  $p > 0.05$ ) after alpha adjustment (adjust = Tukey, SAS). Statistics (F-statistic<sub>num. df, den. df</sub>) and significance are provided seed source, location and seed source  $\times$  location effects from Proc Mixed ANOVA.



**Figure 6-3.** Species richness in (a) 2010, (b) 2011, and (c) 2012 for all seeded species combined (mean  $\pm$  1 s.e.m.). Upper-cases letters indicate significant differences among locations. Statistics and significance follow Fig. 2.



**Figure 6-4.** Nonmetric multidimensional scaling (NMDS) ordinations for plant community structure with statistics from perMANOVA (R: “Adonis”) and stress (Statistics and significance follow Fig. 2). Lines connect points (different seed source treatments within common gardens) to common garden location.



**Figure 6-5.** Total aboveground biomass for all seed species combined in (a) 2010, (b) 2011, and (c) 2012 (mean  $\pm$  1 s.e.m.). Upper-cases letters indicate significant differences among locations.

Statistics and significance follow Fig. 2.

## **Chapter 7 - Concluding Remarks & Recommendations**

Restoration is an optimistic exercise. It attempts to recreate characteristics of natural systems that developed over long periods of time within the space of several years, or perhaps a lifetime. Not only that, restoration attempts to achieve outcomes from different starting points under different environmental conditions. There are many factors that determine the relative success of restoration, of which this dissertation addresses only a small fraction. The combinations of variation among species and genotypes that could be utilized, the range of environmental conditions that could be encountered across space and through time, and the specifics of restoration practices that might be used (timing of seeding, intensity of seeding, prescription of fire or grazing, use of biocides, manipulation of soil nutrient status) are difficult to fathom. Still, this research points towards substantive recommendations, and adds to understanding about how restoration might proceed in a world changing at a pace that rivals or exceeds the pace of restoration ecological research. Refereed conclusions and recommendations may be sought from the individual chapters. I finish here with my personal sense of what is important to take away from this work.

First, restoration can be successful. This may seem a simple statement, but the scope of the problem and the literature reviewed in Chapter 2 suggests the contrary. Chapter 2 demonstrated that restored prairies can recover many of the characteristics of nearby native prairies within several years, including native species cover, low exotic species cover, and mean coefficient of conservatism, which is measure of species that are associated with remnant grasslands. Restored prairies had relatively fewer species with early flowering phenologies, but this may be due to a lack of such species in late season seed harvests. In contrast, richness of late-flowering species was greater on restored than remnant prairies. Late-flowering species'

seeds were captured by fall seed harvests and the collected seed was pooled from remnants with different species compositions. However, restoration success, measured in terms of richness, survival, and productivity clearly depends on environmental conditions, as demonstrated by strong differences in establishment and survival among different restoration sites (Chapters 5 & 6). Investigating methods for increasing the predictability of restoration outcomes across variable environments should be a research priority.

While I did not find that species richness influenced stability to drought in terms of seeded species cover or aboveground biomass, relatively rich restoration plantings had greater sown species cover and lower cover of adventitious species both with and without drought (Chapter 3), and the functional groups that were the most resistant to drought didn't necessarily exhibit the greatest recovery (Chapter 4). Both observations point to the importance of trait variation in seed mixtures.

Seed source had no generalizable effects on restoration outcomes (Chapters 5 & 6). Plant communities derived from mixed sources, however, tended to exhibit intermediate responses. They were neither composed of solely the worst nor solely the best establishing sources. Hence, utilizing seed from multiple, broad-ranging sources of seed may increase the predictability of restoration outcomes across sites that differ in environmental conditions.

Variation, both among species and within species, emerges from these chapters as an important factor in restoration establishment and responses of restored grasslands to variable environments. Recommendations for restoration are as follows: 1) Utilize as many species as practical and appropriate for the site. This generally enhances restoration establishment (Chapter 3). 2) In the process of designing seed mixtures, include species from a variety of functional groups. This may mean including grasses and forbs, for which the responses to drought differ



(Chapter 4), or both early- and late-flowering species to maximize richness (Chapter 2). 3)

Within species, use a variety of sources. This will minimize dependence on single sources, local or not, that might perform poorly. While seeds for many species can be difficult and costly to acquire, allowing for the use of non-local seed should increase availability of some species for particular projects. These practices also comprise an intuitive pre-emptive response to global change. We can coarsely predict some environmental changes (e.g. increased temperature, increased frequency of drought), but we cannot predict the precise magnitude of changes that will result from human activities, nor do we yet have the ability to predict all changes and their interactions simultaneously. If restoration outcomes are to be relatively self-sustaining, restoration in the present needs to account for both current and future conditions. One simple way to do this, when future conditions are unknown, is to equip restored plant communities with as much trait variation as possible within and among species.

## Appendix A - Chapter 2: Species Encountered, Cover, and Designations

Note: Cover data used for analyses in this study was submitted to the Konza LTER Program.

**Table A-1.** Species Encountered and Designations: N = native (\* indicates native trees not included in native analyses), Ex = Exotic (not native to Iowa), An = annual, B = Biennial, P = Perennial, E = Early Phenology (most flowering before June, 21), L = Late Phenology (Most flowering after June 21). Sites are given by restoration age or remnant where J = Judson, O = Owens, T = Tuel with modified Whittaker sampling scale in parentheses.

Species	Site and (Smallest Scale Encountered in m <sup>2</sup> )	Designations		
<i>Acer saccharinum</i>	J(1)	N*	P	E
<i>Achillea millefolium</i>	O(1),T(1),J(1),4(1000),4(10),9(1),10(1)	N	P	E
<i>Agrostis stolonifera</i>	7(1)	Ex	P	E
<i>Ambrosia artimisiifolia</i>	J(1),4(1),7(1),10(1000),11(1)	N	An	L
<i>Ambrosia trifida</i>	O(10)	N	An	L
<i>Amorpha canescens</i>	O(1),T(1),J(1),4(1),6(1),10(1),11(1)	N	P	L
<i>Amphicarpaea bracteata</i>	O(1)	N	P	L
<i>Andropogon gerardii</i>	O(1),T(1),J(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Anemone canadensis</i>	O(1)	N	P	L
<i>Anemone cylindrica</i>	T(1),4(1),7(1),9(1),10(1),11(1)	N	P	E
<i>Antennaria neglecta</i>	T(1000),J(1)	N	P	E
<i>Apocynum cannabinum</i>	T(1000),J(1),9(10)	N	P	L
<i>Artemisia ludoviciana</i>	T(10),J(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Asclepias amplexicaulis</i>	J(10)	N	P	L
<i>Asclepias syriaca</i>	O(1000),T(100),4(1)	N	P	L
<i>Asclepias verticillata</i>	T(1),J(1),4(1),7(1)	N	P	L
<i>Astragalus canadensis</i>	O(10),4(1000),10(1),11(1)	N	P	L
<i>Astragalus crassicaarpus</i>	4(1),11(1000)	N	P	E
<i>Baptisia alba</i>	4(1),7(1),9(1),10(1),11(1)	N	P	L

<i>Baptisia bracteata</i>	O(10),T(1),J(1000),4(1),6(1),7(10),9(1),10(100),11(1)	N	P	E
<i>Barbarea vulgaris</i>	4(10)	Ex	B	E
<i>Bouteloua curtipendula</i>	T(1),J(1),4(1),6(1),7(1),9(1),10(100)	N	P	L
<i>Bouteloua hirsuta</i>	J(1)	N	P	L
<i>Brickellia kuhnioides</i>	4(1),7(1000),9(1000),10(1),11(1)	N	P	L
<i>Bromus inermis</i>	O(10),4(1),6(1),7(1000),9(1),10(1),11(1)	Ex	P	E
<i>Cacalia tuberosa</i>	6(1000),7(10),11(1)	N	P	L
<i>Caenothus americanus</i>	10(1000)	N	P	E
<i>Calyophus serrulatus</i>	T(100)	N	P	L
<i>Calystegia sepium</i>	O(1),6(1),9(1),11(1000)	N	P	L
<i>Capsella bursa-pastoris</i>	4(1)	Ex	An	E
<i>Carex brevior</i>	O(10),4(100),6(100),7(10),11(1000)	N	P	E
<i>Carex davisii</i>	O(1)	N	P	E
<i>Carex haydenii</i>	O(1)	N	P	E
<i>Carex inops</i>	O(1),T(1),J(1)	N	P	E
<i>Carex meadii</i>	O(1),T(1)	N	P	E
<i>Carex stricta</i>	O(10)	N	P	E
<i>Ceanothus americanus</i>	O(1),T(1)	N	P	E
<i>Chamaecrista fasciculata</i>	O(1),J(1),6(1),7(1000),9(1),10(1),11(10)	N	An	L
<i>Chenopodium album</i>	4(1)	Ex	An	L
<i>Cirsium arvense</i>	4(1)	Ex	P	L
<i>Cirsium discolor</i>	O(10)	N	B	L
<i>Cirsium vulgare</i>	4(1)	Ex	B	L
<i>Comandra umbellata</i>	O(1),T(1)	N	P	E
<i>Conyza canadensis</i>	J(100),4(1),7(1)	N	An	L
<i>Coreopsis palmata</i>	O(1),6(1),7(1),9(100),10(1)	N	P	L
<i>Craetagus sp.</i>	J(1)	N*	P	L
<i>Dalea candida</i>	O(100),T(1),4(1),6(1),7(1),9(1),10(10),11(1)	N	P	L
<i>Dalea purpurea</i>	O(1000),T(1),J(10),4(1),7(10),9(1),10(1),11(1)	N	P	L
<i>Daucus carota</i>	4(100)	Ex	B	L

<i>Delphinium virescens</i>	O(1000),J(1),4(1),6(1),9(1),11(1000)	N	P	E
<i>Desmodium canadense</i>	T(1),4(1),6(1),7(1),9(1000),10(1)	N	P	L
<i>Desmodium illinoense</i>	O(10),4(1),10(1),11(1)	N	P	L
<i>Dicanthelium acuminatum</i>	T(1),J(1)	N	P	E
<i>Dicanthelium oligosanthes</i>	O(1),T(10),J(1),4(100),9(100)	N	P	E
<i>Echinacea pallida</i>	O(100),T(1),J(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Eleocharis compressa</i>	O(1)	N	P	E
<i>Elymus canadensis</i>	O(10),T(1),J(1000),4(1),9(10),11(100)	N	P	E
<i>Equisetum arvense</i>	O(1),T(10)	N	P	N/A
<i>Equisetum hyemale</i>	O(1),11(1000)	N	P	N/A
<i>Erigeron annuus</i>	4(1),11(1)	N	An	L
<i>Eryngium yuccifolium</i>	O(1),6(1),7(1),10(1),11(1)	N	P	L
<i>Euphorbia corollata</i>	O(1),T(1),6(1),9(100)	N	P	L
<i>Euthamia graminifolia</i>	O(1)	N	P	L
<i>Festuca aurundinacea</i>	4(1)	Ex	P	E
<i>Galium boreale</i>	O(1)	N	P	L
<i>Gaura biennis</i>	O(10),11(100)	N	B	L
<i>Gentiana puberulenta</i>	O(1000),T(1000),6(1000),11(1000)	N	P	L
<i>Helianthemum canadense</i>	J(1)	N	P	E
<i>Helianthus grosseserratus</i>	O(1),4(10),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Helianthus pauciflorus</i>	O(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Helianthus tuberosus</i>	9(1)	N	P	L
<i>Heliopsis helianthoides</i>	O(1),T(1),4(1),6(1),7(1),9(1),10(10),11(1)	N	P	L
<i>Hesperostipa spartea</i>	O(1),T(1),J(1)	N	P	E
<i>Heuchera richardsonii</i>	6(100)	N	P	E
<i>Hieraceum longipilum</i>	O(1)	N	P	L
<i>Hypoxis hirsuta</i>	O(1)	N	P	E
<i>Koeleria macrantha</i>	4(1),6(1),10(1000)	N	P	E
<i>Lactuca pulchella</i>	T(1000)	N	B	L
<i>Lactuca serriola</i>	7(1),9(1)	Ex	B	L

<i>Lespedeza capitata</i>	T(1),J(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Liatris aspera</i>	J(1),4(10),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Liatris punctata</i>	4(1),11(100)	N	P	L
<i>Liatris pycnostachya</i>	O(1),4(1000),6(1),7(1),9(1),10(1),11(10)	N	P	L
<i>Liatris squarrosa</i>	J(1),4(10),6(1),9(1),10(1),11(1)	N	P	L
<i>Lillium philadelphicum</i>	O(1)	N	P	E
<i>Lithospermum canescens</i>	O(1000),T(100)	N	P	E
<i>Lobelia spicata</i>	O(10),T(1),4(1)	N	P	L
<i>Melilotus officinalis</i>	T(1),4(1),7(1000),9(1000),11(1000)	Ex	B	L
<i>Monarda fistulosa</i>	T(1),4(1),6(1),9(1),10(1),11(1)	N	P	L
<i>Morus alba</i>	T(100),4(10)	Ex	P	L
<i>Oenothera biennis</i>	J(100),4(1),11(100)	N	B	L
<i>Oligoneuron rigidum</i>	O(1),T(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Onosmodium bejariense</i>	4(100)	N	P	L
<i>Oxalis stricta</i>	4(1)	N	An	E
<i>Oxalis violacea</i>	O(1),T(10),J(1)	N	P	E
<i>Panicum virgatum</i>	O(1),T(1),4(1),6(1),7(1),9(1),10(100),11(1)	N	P	L
<i>Pastinaca sativa</i>	7(1000)	Ex	P	E
<i>Pedicularis canadensis</i>	O(1)	N	P	E
<i>Phleum pratense</i>	4(1)	Ex	P	E
<i>Phlox pilosa</i>	O(1),6(1)	N	P	E
<i>Phalaris arundinacea</i>	O(1)	Ex	P	L
<i>Physalis virginica</i>	O(100),T(1),J(1)	N	P	L
<i>Plantago major</i>	4(1)	Ex	P	L
<i>Poa pratensis</i>	T(1),J(100),4(1),6(1),7(1),9(1)	Ex	P	E
<i>Polytaenia nuttallii</i>	4(100),6(100)	N	P	E
<i>Potentilla arguta</i>	T(10),4(1),6(100),7(1),9(100),10(1),11(1)	N	P	L
<i>Prenanthes aspera</i>	T(1)	N	P	L
<i>Prunus americana</i>	T(1),4(1)	N*	P	L
<i>Pycnanthemum tenuifolium</i>	O(1)	N	P	L

<i>Pycnanthemum virginicum</i>	O(1),4(10),11(1)	N	P	L
<i>Quercus macrocarpa</i>	J(1000)	N*	P	L
<i>Ratibida pinnata</i>	O(10),T(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Rosa arkansana</i>	O(1),T(1),J(1),9(1000)	N	P	E
<i>Rudbeckia hirta</i>	T(10),4(1),9(1),11(1)	N	B	L
<i>Rumex crispus</i>	10(10),11(1000)	Ex	P	E
<i>Schizachyrium scoparium</i>	O(1),T(1),J(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Silphium integrifolium</i>	O(1),J(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Silphium laciniatum</i>	O(1),4(100),6(1),7(1),9(1),10(1),11(10)	N	P	L
<i>Silphium perfoliatum</i>	4(10),9(100),11(100)	N	P	L
<i>Simphyotrichum ericoides</i>	O(1),T(1),J(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Simphyotrichum laevum</i>	O(1),T(1),4(1),6(1),9(100),10(10),11(1)	N	P	L
<i>Simphyotrichum novae-angliae</i>	6(1),7(1),9(1000)	N	P	L
<i>Simphyotrichum oolentangiense</i>	O(1),T(1),4(1),6(1),7(1),10(1),11(1)	N	P	L
<i>Simphyotrichum pilosum</i>	J(1),4(1),6(1),9(1),10(1),11(1)	N	P	L
<i>Simphyotrichum sericeum</i>	6(100),10(10)	N	P	L
<i>Sisyrinchium campestre</i>	O(1),T(1),4(1),11(1000)	N	P	E
<i>Solidago canadensis</i>	O(1),4(10),7(1),11(100)	N	P	L
<i>Solidago missouriensis</i>	O(1),T(1),6(1),7(1),9(10),10(1)	N	P	L
<i>Solidago nemoralis</i>	10(1000)	N	P	L
<i>Solidago speciosa</i>	T(1),4(100),6(1),7(1),9(10),10(1)	N	P	L
<i>Sorghastrum nutans</i>	O(1),T(1),J(10),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	L
<i>Spartina pectinata</i>	O(1)	N	P	L
<i>Sporobolis heterolepis</i>	O(1),J(1),4(1),6(1),7(1),10(1),11(1)	N	P	L
<i>Taraxium officinale</i>	4(1),6(1),9(1000),10(1),11(10)	Ex	P	E
<i>Tradescantia bracteata</i>	O(1),4(10),9(100)	N	P	E
<i>Tradescantia ohioensis</i>	J(1),4(1),6(1),7(1),9(1),10(1),11(1)	N	P	E
<i>Trifolium pratense</i>	T(1)	Ex	P	E
<i>Ulmus americana</i>	T(1000)	N*	P	E
<i>Verbena stricta</i>	J(1),4(1)	N	P	L

<i>Verbena urticifolia</i>	4(1)	N	P	L
<i>Vernonia baldwinii</i>	T(1),6(1),7(1),10(1),11(10)	N	P	L
<i>Veronica peregrina</i>	4(1),7(1)	N	An	E
<i>Veronicastrum virginicum</i>	O(10),4(1000)	N	P	L
<i>Viola pedata</i>	O(100)	N	P	E
<i>Viola pedatifida</i>	O(1),T(1)	N	P	E
<i>Viola sororia</i>	O(1)	N	P	E
<i>Zizia aurea</i>	O(1),4(1),6(1),7(1),9(1),10(10),11(1)	N	P	E

**Table A-2.** Avg. cover by species (among 10 1m<sup>2</sup> subplots/prairie) for the three remnant prairies.

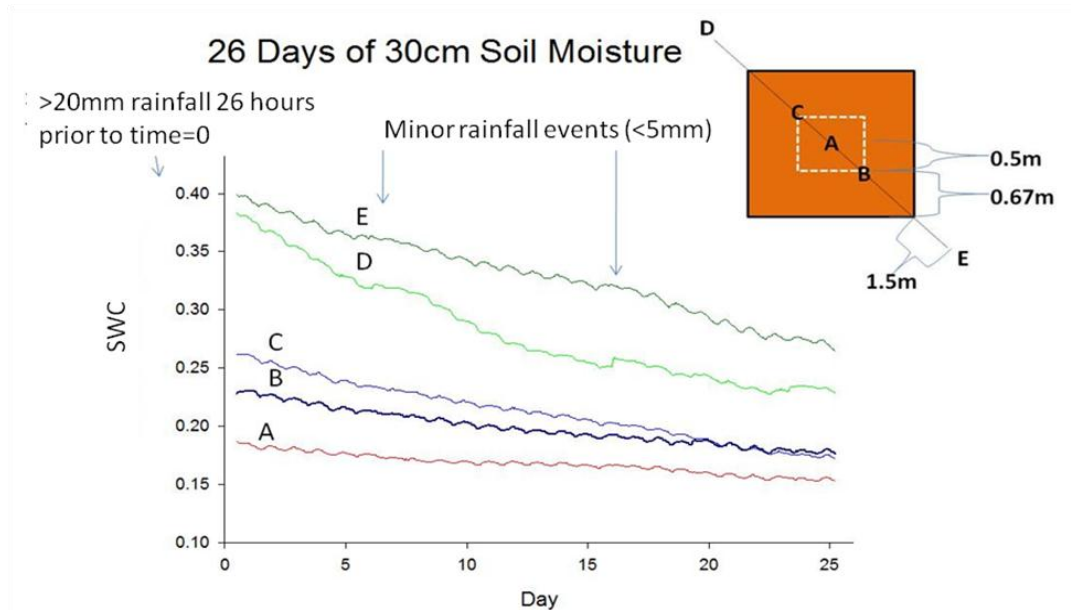
Judson Species	Judson Cover	Owens Species	Owens Cover	Tuel Species	Tuel Cover
<i>Achillea millefolium</i>	0.2	<i>Achillea millefolium</i>	0.2	<i>Achillea millefolium</i>	0.2
<i>Ambrosia artemisifolia</i>	9.2	<i>Amorpha canescens</i>	1.1	<i>Amorpha canescens</i>	8.4
<i>Amorpha canescens</i>	1.5	<i>Amphicarpa bracteata</i>	1.6	<i>Andropogon gerardii</i>	24.5
<i>Andropogon gerardii</i>	5.8	<i>Andropogon gerardii</i>	5	<i>Anemone cylindrica</i>	0.9
<i>Antennaria neglecta</i>	0.4	<i>Anemone canadensis</i>	0.8	<i>Antennaria neglecta</i>	0.9
<i>Apocynum cannabinum</i>	0.4	<i>Aster azureus</i>	1.1	<i>Apocynum cannabinum</i>	0.1
<i>Artemisia ludoviciana</i>	23.5	<i>Aster ericoides</i>	0.7	<i>Asclepias verticillata</i>	0.1
<i>Asclepias verticillata</i>	0.2	<i>Aster laevis</i>	0.2	<i>Aster azureus</i>	0.6
<i>Aster ericoides</i>	11	<i>Calystegia sepium</i>	0.1	<i>Aster ericoides</i>	9.7
<i>Aster pilosa</i>	0.2	<i>Carex davisii</i>	9.8	<i>Aster laevis</i>	1
<i>Baptisia bracteata</i>	0.2	<i>Carex haydenii</i>	0.4	<i>Baptisia bracteata</i>	0.7
<i>Bouteloua curtipendula</i>	6.2	<i>Carex inops heliophila</i>	0.1	<i>Bouteloua curtipendula</i>	0.4
<i>Carex inops heliophila</i>	9	<i>Carex meedii</i>	4.6	<i>Carex inops heliophila</i>	6.5
<i>Chamaecrista fasciculata</i>	1.2	<i>Ceanothus americanus</i>	0.1	<i>Carex meedii</i>	10.9
<i>Delphinium virescens</i>	1.1	<i>Chamaecrista fasciculata</i>	0.7	<i>Ceanothus americanus</i>	0.7
<i>Dicanthelium acuminatum</i>	1.1	<i>Comandra umbellata</i>	6.1	<i>Comandra umbellata</i>	12.2
<i>Dicanthelium oligosanthes</i>	1.3	<i>Coreopsis palmata</i>	1.7	<i>Dalea candida</i>	0.9
<i>Echinacea pallida</i>	2.9	<i>Dicanthelium oligosan</i>	3.5	<i>Dalea purpurea</i>	0.5
<i>Helianthemum canadense</i>	0.8	<i>Eleocharis compressa</i>	1.2	<i>Desmodium canadense</i>	0.5
<i>Hesperostipa spartea</i>	1.6	<i>Equisetum arvense</i>	0.7	<i>Dicanthelium acumina</i>	3.1
<i>Lespedeza capitata</i>	4.7	<i>Equisetum hyemense</i>	0.1	<i>Echinacea pallida</i>	5.5
<i>Liatis aspera</i>	1.6	<i>Eryngium yuccifolium</i>	0.4	<i>Elymus canadensis</i>	0.9
<i>Liatis squarrosa</i>	2.2	<i>Euphorbia corollata</i>	0.3	<i>Euphorbia corollata</i>	1.9
<i>Oxalis violacea</i>	0.4	<i>Euthamia graminifolia</i>	0.2	<i>Heliopsis helianthoides</i>	5.2
<i>Physalis virginica</i>	0.2	<i>Galium boreale</i>	0.3	<i>Hesperostipa spartea</i>	4.5
<i>Rosa carolina</i>	1.6	<i>Helianthus grosseserrata</i>	5.1	<i>Lactuca pulchellus</i>	0.1
<i>Schizachyrium scoparium</i>	67	<i>Helianthus pauciflorus</i>	15.2	<i>Lespedeza capitata</i>	1.1
<i>Sisyrinchium campestre</i>	0.2	<i>Heliopsis helianthoides</i>	0.5	<i>Lobelia spicata</i>	0.1
<i>Sporobolus heterolepis</i>	1.5	<i>Hesperostipa spartea</i>	3.2	<i>Monarda fistulosa</i>	1.4
<i>Tradescantia ohioensis</i>	2.8	<i>Hieraceum longipilum</i>	0.1	<i>Panicum virgatum</i>	0.4
<i>Verbena stricta</i>	0.3	<i>Hypoxis hirsuta</i>	1.4	<i>Physalis virginica</i>	0.5
<i>Craetagus calpodendron</i>	1.2	<i>Liatis pycnostachya</i>	0.5	<i>Prenanthes aspera</i>	0.3
<i>Acer saccharinum</i>	0.1	<i>Lillium philadelphicum</i>	0.3	<i>Ratibida pinnata</i>	2.3
		<i>Oxalis violacea</i>	0.4	<i>Rosa carolina</i>	0.7
		<i>Panicum virgatum</i>	1.2	<i>Schizachyrium scoparium</i>	20.1
		<i>Pedicularis canadensis</i>	1.9	<i>Sisyrinchium campestre</i>	1
		<i>Phlox pilosa</i>	1	<i>Solidago missouriensis</i>	0.2
		<i>Pycnanthemum tenuifolium</i>	0.5	<i>Solidago rigida</i>	1
		<i>Pycnanthemum virginicum</i>	1	<i>Solidago speciosa</i>	0.2
		<i>Rosa carolina</i>	0.2	<i>Sorghastrum nutans</i>	40
		<i>Schizachyrium scoparium</i>	6.3	<i>Vernonia baldwinii</i>	1.2
		<i>Silphium integrifolium</i>	2.6	<i>Viola pedatifida</i>	0.3
		<i>Silphium laciniata</i>	0.1	<i>Poa pratensis</i>	2.7
		<i>Sisyrinchium campestre</i>	0.3	<i>Prunus virginiana</i>	0.1
		<i>Solidago canadensis</i>	2	<i>Trifolium sp.</i>	0.5
		<i>Solidago missouriensis</i>	0.3	<i>Melilotus alba</i>	0.2
		<i>Solidago rigida</i>	0.6		
		<i>Sorghastrum nutans</i>	1.3		
		<i>Spartina pectinata</i>	4.3		
		<i>Sporobolus heterolepis</i>	4.7		
		<i>Tradescantia bracteata</i>	0.3		
		<i>Viola pedatifida</i>	0.2		
		<i>Viola sororia</i>	0.2		
		<i>Zizia aurea</i>	2.4		
		<i>Phalaris aurundinacea</i>	1.2		



**Table A-3.** Avg. cover by species (among 10 1m<sup>2</sup> subplots/prairie) for the six restored prairies.

1998 Species	1998 Cover	2000 Species	2000 Cover	2003 Species	2003 Cover	2005 Species	2005 Cover
<i>Ambrosia artemisiifolia</i>	0.6	<i>Ambrosia artemisiifolia</i>	0.8	<i>Amarpha canescens</i>	1.9	<i>Achillea millefolium</i>	0.2
<i>Amarpha canescens</i>	1.5	<i>Andropogon gerardii</i>	42.2	<i>Andropogon gerardii</i>	28.5	<i>Ambrosia artemisiifolia</i>	2
<i>Andropogon gerardii</i>	24.5	<i>Anenome cylindrica</i>	0.1	<i>Artemisia ludoviciana</i>	1	<i>Amarpha canescens</i>	0.8
<i>Anenome cylindrica</i>	0.2	<i>Artemisia ludoviciana</i>	2.9	<i>Aster azureus</i>	1	<i>Andropogon gerardii</i>	10.8
<i>Artemisia ludoviciana</i>	5.1	<i>Symphyotrichum ericoides</i>	0.6	<i>Aster ericoides</i>	6	<i>Anenome cylindrica</i>	0.1
<i>Aster azureus</i>	0.2	<i>Symphyotrichum pilosum</i>	0.2	<i>Aster pilosus</i>	0.3	<i>Asclepias syriaca</i>	0.5
<i>Aster ericoides</i>	6.1	<i>Baptisia alba</i>	0.5	<i>Aster laevis</i>	0.6	<i>Asclepias verticillata</i>	0.5
<i>Aster laevis</i>	0.1	<i>Baptisia bracteata</i>	0.1	<i>Baptisia bracteata</i>	1.2	<i>Aster azureus</i>	1.7
<i>Aster pilosus</i>	1.3	<i>Bouteloua curtipendula</i>	0.9	<i>Bouteloua curtipendula</i>	0.1	<i>Aster ericoides</i>	0.4
<i>Astragalus canadensis</i>	0.2	<i>Calystegia sepium</i>	0.3	<i>Calystegia sepium</i>	0.1	<i>Aster laevis</i>	0.3
<i>Baptisia alba</i>	0.3	<i>Chamaecrista fasciculata</i>	0.6	<i>Chamaecrista fasciculata</i>	1.7	<i>Aster pilosus</i>	0.6
<i>Baptisia bracteata</i>	0.4	<i>Dalea candida</i>	0.3	<i>Coreopsis palmata</i>	1.3	<i>Astragalus crassicaeris</i>	0.4
<i>Brickellia kuhnioides</i>	1.1	<i>Dalea purpurea</i>	0.5	<i>Dalea candida</i>	0.1	<i>Baptisia alba</i>	0.1
<i>Cacalia tuberosa</i>	0.1	<i>Delphinium virascens</i>	0.3	<i>Delphinium virascens</i>	0.3	<i>Baptisia bracteata</i>	0.3
<i>Coreopsis palmata</i>	0	<i>Echinacea pallida</i>	1.9	<i>Desmodium canadense</i>	0.5	<i>Bouteloua curtipendula</i>	4.9
<i>Dalea candida</i>	1.9	<i>Helianthus pauciflorus</i>	12.7	<i>Echinacea pallida</i>	2.9	<i>Brickellia kuhnioides</i>	0.3
<i>Dalea purpurea</i>	1	<i>Helianthus tuberosus</i>	1.2	<i>Eryngium yuccifolium</i>	4.3	<i>Conyza canadensis</i>	11.6
<i>Desmodium illinoense</i>	0.3	<i>Helianthus grosseserratus</i>	0.3	<i>Helianthus grosseserratus</i>	0.6	<i>Dalea candida</i>	1.2
<i>Echinacea pallida</i>	2.4	<i>Heliopsis helianthoides</i>	0.1	<i>Helianthus pauciflorus</i>	1.9	<i>Dalea purpurea</i>	2.3
<i>Equisetum hyemale</i>	0.1	<i>Lespedeza capitata</i>	0.5	<i>Heliopsis helianthoides</i>	0.4	<i>Delphinium virascens</i>	0.5
<i>Erigeron annuus</i>	0.1	<i>Liatris aspera</i>	0.2	<i>Koeleria cristata</i>	0.5	<i>Desmodium canadense</i>	1.9
<i>Eryngium yuccifolium</i>	0.7	<i>Liatris pycnostachya</i>	0.2	<i>Lespedeza capitata</i>	2.3	<i>Desmodium illinoense</i>	0.5
<i>Helianthus grosseserratus</i>	2.5	<i>Liatris squarrosa</i>	0.5	<i>Liatris aspera</i>	0.5	<i>Echinacea pallida</i>	2.4
<i>Helianthus pauciflorus</i>	0.2	<i>Monarda fistulosa</i>	1.3	<i>Liatris pycnostachya</i>	1.2	<i>Elymus canadensis</i>	2
<i>Heliopsis helianthoides</i>	0.1	<i>Panicum virgatum</i>	0.6	<i>Liatris squarrosa</i>	1.8	<i>Erigeron annuus</i>	5.1
<i>Lespedeza capitata</i>	2.3	<i>Ratibida pinnata</i>	3	<i>Monarda fistulosa</i>	0.3	<i>Heliopsis helianthoides</i>	1.9
<i>Liatris aspera</i>	0.3	<i>Rudbeckia hirta</i>	4.6	<i>Panicum virgatum</i>	0.3	<i>Koeleria macrantha</i>	0.2
<i>Liatris squarrosa</i>	0.1	<i>Schizachyrium scoparium</i>	52.5	<i>Phlox pilosa</i>	0.1	<i>Lespedeza capitata</i>	0.7
<i>Monarda fistulosa</i>	0.2	<i>Silphium integrifolium</i>	0.4	<i>Ratibida pinnata</i>	1.3	<i>Liatris punctata</i>	0.2
<i>Panicum virgatum</i>	0.8	<i>Silphium laciniatum</i>	0.5	<i>Schizachyrium scoparium</i>	36	<i>Lobelia spicata</i>	0.1
<i>Potentilla arguta</i>	0.1	<i>Solidago rigida</i>	9	<i>Silphium integrifolium</i>	1.6	<i>Monarda fistulosa</i>	4.7
<i>Pycnanthemum virginicum</i>	1.5	<i>Sorghastrum nutans</i>	11.8	<i>Silphium laciniatum</i>	1	<i>Oenothera biennis</i>	0.2
<i>Ratibida pinnata</i>	3.3	<i>Tradescantia ohioensis</i>	1.1	<i>Solidago missouriensis</i>	1.6	<i>Oxalis stricta</i>	1.7
<i>Rudbeckia hirta</i>	0.1	<i>Zizia aurea</i>	1.7	<i>Solidago nemoralis</i>	0.7	<i>Panicum virgatum</i>	0.4
<i>Schizachyrium scoparium</i>	58	<i>Bromus inermis</i>	0.5	<i>Solidago rigida</i>	29.3	<i>Potentilla arguta</i>	0.1
<i>Silphium integrifolium</i>	0.5	<i>Poa pratensis</i>	0.5	<i>Solidago speciosa</i>	1.8	<i>Ratibida pinnata</i>	2.5
<i>Solidago rigida</i>	1.1	<b>2002 Species</b>	<b>2002 Cover</b>	<i>Sorghastrum nutans</i>	20.8	<i>Rudbeckia hirta</i>	0.9
<i>Sorghastrum nutans</i>	13	<i>Andropogon gerardii</i>	13.3	<i>Sporobolus heterolepus</i>	1.2	<i>Schizachyrium scoparium</i>	8.4
<i>Sporobolus heterolepus</i>	1.2	<i>Anenome cylindrica</i>	0.2	<i>Tradescantia ohioensis</i>	0.6	<i>Sisyrinchium campestre</i>	0.4
<i>Tradescantia ohioensis</i>	1.3	<i>Artemisia ludoviciana</i>	4.8	<i>Vernonia baldwinii</i>	0.1	<i>Solidago rigida</i>	2.8
<i>Zizia aurea</i>	0.8	<i>Asclepias verticillata</i>	0.3	<i>Zizia aurea</i>	0.2	<i>Sorghastrum nutans</i>	15.3
<i>Bromus inermis</i>	0.2	<i>Symphyotrichum oolentangiense</i>	1.2	<i>Poa pratensis</i>	2	<i>Sporobolus heterolepus</i>	0.2
<b>1999 Species</b>	<b>1999 Cover</b>	<i>Symphyotrichum ericoides</i>	5.7	<i>Bromus inermis</i>	0.2	<i>Tradescantia ohioensis</i>	0.4
<i>Achillea millefolium</i>	0.4	<i>Symphyotrichum novae-angliae</i>	0.3	<i>Taraxium officinale</i>	0.1	<i>Verbena stricta</i>	0.2
<i>Amarpha canescens</i>	12.2	<i>Baptisia alba</i>	2.2			<i>Verbena urtifolia</i>	0.8
<i>Andropogon gerardii</i>	7.7	<i>Bouteloua curtipendula</i>	0.2			<i>Veronica peregrina</i>	0.4
<i>Anenome cylindrica</i>	0.1	<i>Chamaecrista fasciculata</i>	0.3			<i>Zizia aurea</i>	2.5
<i>Artemisia ludoviciana</i>	0.3	<i>Conyza canadensis</i>	0.3			<i>Plantago major</i>	0.2
<i>Aster azureus</i>	1.1	<i>Coreopsis palmata</i>	5.1			<i>Festuca arundinacea</i>	2.4
<i>Aster ericoides</i>	3	<i>Dalea candida</i>	0.3			<i>Cirsium arvense</i>	2.1
<i>Aster pilosus</i>	1.1	<i>Desmodium canadense</i>	0.9			<i>Cirsium vulgare</i>	3
<i>Astragalus canadensis</i>	0.2	<i>Echinacea pallida</i>	5.4			<i>Poa pratensis</i>	3
<i>Baptisia alba</i>	0.2	<i>Eryngium yuccifolium</i>	3.4			<i>Melilotus alba</i>	0.1
<i>Brickellia kuhnioides</i>	0.5	<i>Helianthus grosseserratus</i>	0.3			<i>Bromus inermis</i>	7.4
<i>Chamaecrista fasciculata</i>	0.6	<i>Helianthus pauciflorus</i>	19.5			<i>Taraxium officinale</i>	0.1
<i>Coreopsis palmata</i>	0.4	<i>Heliopsis helianthoides</i>	0.2			<i>Capsella bursa-pastoris</i>	1.3
<i>Dalea purpurea</i>	0.6	<i>Lespedeza capitata</i>	2.2			<i>Chenopodium album</i>	0.8
<i>Desmodium canadense</i>	10.5	<i>Liatris aspera</i>	0.3			<i>Phleum pratense</i>	0.3
<i>Desmodium illinoensis</i>	6.2	<i>Liatris pycnostachya</i>	2.8				
<i>Echinacea pallida</i>	1.8	<i>Panicum virgatum</i>	0.4				
<i>Eryngium yuccifolium</i>	0.2	<i>Potentilla arguta</i>	0.3				
<i>Helianthus grosseserratus</i>	0.2	<i>Ratibida pinnata</i>	3				
<i>Helianthus pauciflorus</i>	0.7	<i>Schizachyrium scoparium</i>	13				
<i>Lespedeza capitata</i>	7.8	<i>Silphium integrifolium</i>	0.5				
<i>Liatris aspera</i>	1.7	<i>Silphium laciniatum</i>	0.9				
<i>Liatris pycnostachya</i>	0.4	<i>Solidago canadensis</i>	0.3				
<i>Liatris squarrosa</i>	1.3	<i>Solidago missouriensis</i>	0.6				
<i>Monarda fistulosa</i>	0.6	<i>Solidago rigida</i>	18.8				
<i>Potentilla arguta</i>	0.7	<i>Solidago speciosa</i>	0.2				
<i>Ratibida pinnata</i>	1.2	<i>Sorghastrum nutans</i>	13.8				
<i>Schizachyrium scoparium</i>	79	<i>Sporobolus heterolepus</i>	3				
<i>Silphium integrifolium</i>	0.2	<i>Tradescantia ohioensis</i>	1.3				
<i>Silphium laciniatum</i>	0.8	<i>Vernonia baldwinii</i>	0.3				
<i>Solidago nemoralis</i>	1.6	<i>Veronica peregrina</i>	0.2				
<i>Solidago rigida</i>	1.1	<i>Zizia aurea</i>	0.3				
<i>Solidago speciosa</i>	3.3	<i>Lactuca scariola</i>	0.1				
<i>Sorghastrum nutans</i>	7.5	<i>Agrostis stolonifera</i>	1.2				
<i>Sporobolus heterolepus</i>	0.4	<i>Poa pratensis</i>	2.1				
<i>Tradescantia ohioensis</i>	0.9						
<i>Vernonia baldwinii</i>	0.3						
<i>Bromus inermis</i>	0.1						
<i>Taraxium officinale</i>	0.1						

## Appendix B - Chapters 3 & 4: Volumetric SWC, view of shelters, and species list



**Figure B-1.** 30 cm SWC from 6/27/09 to 7/23/09 at five points indicated on inset. Inset orange shading represents the area under the shelter and the white square represents the drought treatment vegetation sampling area. Line A = SWC at center of rainout shelter. Lines B and C = SWC at corners of vegetation sampling area. Lines D and E = SWC 1.5 m away from opposite corners of the rainout shelter. Rainfall events are indicated (estimated from radar precipitation estimates).



**Figure B-2.** View of shelters within experimental plots (permission Todd Harders and Shawn Harders).

**Table B-1.** All species encountered (sown and encountered denoted by \*, all listed non-seeded species were encountered) with native / exotic status, perennial / biennial / annual (p / b / a) life form and functional group [C<sub>4</sub>, C<sub>3</sub> graminoid (= C<sub>3</sub>) or forb] indicated. Nomenclature and life forms for taxa follow the United States Department of Agriculture Plants Database ([www.plants.usda.gov](http://www.plants.usda.gov), accessed 6/2011). All *Elymus* species were definitively observed, but these were lumped together for all analyses in the main text (see Methods). Records were not available from TNC for seeding densities at the species level.

Species	Native/Exotic	Seeded	Life Form	Funct. Group
<i>Achillea millefolium</i> *	native	yes	p	Forb
<i>Allium canadense</i>	native	yes	p	Forb
<i>Ambrosia psilostachya</i>	native	no	p	forb
<i>Ambrosia trifida</i>	native	no	a	forb
<i>Amorpha canescens</i>	native	yes	p	Forb
<i>Andropogon gerardii</i> *	native	yes	p	C <sub>4</sub>
<i>Anemone canadensis</i>	native	yes	p	Forb
<i>Artemisia ludoviciana</i> *	native	yes	p	Forb

<i>Asclepias speciosa</i>	native	yes	p	Forb
<i>Asclepias syriaca</i> *	native	yes	p	Forb
<i>Asclepias verticillata</i> *	native	yes	p	Forb
<i>Astragalus canadensis</i> *	native	yes	p	Forb
<i>Bouteloua curtipendula</i> *	native	yes	p	C <sub>4</sub>
<i>Brickellia eupatorioides</i>	native	yes	p	Forb
<i>Calamagrostis canadensis</i>	native	yes	p	C <sub>3</sub>
<i>Callirhoe involucrata</i>	native	yes	p	Forb
<i>Calylophus serrulatus</i>	native	yes	p	Forb
<i>Cannabis sativa</i>	exotic	no	a	forb
<i>Carduus nutans</i>	exotic	no	b	forb
<i>Carex brevior</i> *	native	yes	p	C <sub>3</sub>
<i>Carex duriuscula</i>	native	yes	p	C <sub>3</sub>
<i>Carex gravida</i>	native	yes	p	C <sub>3</sub>
<i>Chenopodium album</i>	exotic	no	a	forb
<i>Cirsium discolor</i>	native	no	b	forb
<i>Conium maculatum</i>	exotic	no	b	forb
<i>Convolvulus arvensis</i>	exotic	no	p	forb
<i>Coryza canadensis</i>	native	no	a	forb
<i>Crepis runcinata</i>	native	yes	p	C <sub>3</sub>
<i>Cyperus lupulinus</i>	native	yes	p	C <sub>3</sub>
<i>Cyperus schweinitzii</i>	native	yes	p	C <sub>4</sub>
<i>Dalea candida</i> *	native	yes	p	forb
<i>Dalea purpurea</i> *	native	yes	p	Forb
<i>Delphinium carolinianum</i>	native	yes	p	forb
<i>Desmanthus illinoensis</i> *	native	yes	p	forb

<i>Desmodium illinoense</i>	native	yes	p	forb
<i>Digitaria ischaemum</i>	exotic	no	a	C <sub>4</sub>
<i>Digitaria cognata</i>	native	yes	p	C <sub>4</sub>
<i>Eleocharis elliptica</i>	native	yes	p	C <sub>3</sub>
<i>Elymus canadensis</i> *	native	yes	p	C <sub>3</sub>
<i>Elymus trachycaulus</i> *	native	yes	p	C <sub>3</sub>
<i>Elymus virginicus</i> *	native	yes	p	C <sub>3</sub>
<i>Eragrostis spectabilis</i>	native	yes	p	C <sub>4</sub>
<i>Eragrostis trichodes</i>	native	yes	p	C <sub>4</sub>
<i>Eupatorium altissimum</i>	native	yes	p	forb
<i>Eustoma exaltatum</i>	native	yes	a	forb
<i>Euthamia graminifolia</i>	native	yes	p	forb
<i>Gaura mollis</i>	native	yes	b	forb
<i>Geum canadense</i> *	native	yes	p	forb
<i>Geum vernum</i>	native	yes	p	forb
<i>Glycyrrhiza lepidota</i> *	native	yes	p	forb
<i>Helianthus annuus</i>	native	no	a	forb
<i>Helianthus grosseserratus</i>	native	yes	p	forb
<i>Helianthus maximiliani</i> *	native	yes	p	forb
<i>Helianthus pauciflorus</i>	native	yes	p	forb
<i>Helianthus petiolaris</i>	native	yes	a	forb
<i>Helianthus tuberosus</i>	native	yes	p	forb
<i>Heliopsis helianthoides</i>	native	yes	p	forb
<i>Hesperostipa comata</i>	native	yes	p	C <sub>3</sub>
<i>Hesperostipa spartea</i>	native	yes	p	C <sub>3</sub>
<i>Heterotheca villosa</i>	native	yes	p	forb

<i>Juncus dudleyi</i>	native	yes	p	C <sub>3</sub>
<i>Koeleria macrantha</i>	native	no	p	C <sub>3</sub>
<i>Lactuca serriola</i>	exotic	no	a	forb
<i>Lepidium campestre</i>	exotic	no	a	forb
<i>Lespedeza capitata</i>	native	yes	p	forb
<i>Liatris lancifolia</i>	native	yes	p	forb
<i>Liatris punctata*</i>	native	yes	p	forb
<i>Liatris squarrosa</i>	native	yes	p	forb
<i>Lithospermum caroliniense</i>	native	yes	p	forb
<i>Lithospermum incisum</i>	native	yes	p	forb
<i>Lotus unifoliolatus*</i>	native	yes	a	forb
<i>Medicago sativa</i>	exotic	no	a	forb
<i>Melilotus officinalis</i>	exotic	no	b	forb
<i>Mimosa nuttallii</i>	native	yes	p	forb
<i>Mirabilis nyctaginea</i>	native	yes	p	forb
<i>Monarda fistulosa*</i>	native	yes	p	forb
<i>Nepeta cataria</i>	exotic	no	p	forb
<i>Oenothera biennis*</i>	native	yes	b	forb
<i>Oenothera rhombipetala</i>	native	yes	b	forb
<i>Oligoneuron rigidum*</i>	native	yes	p	forb
<i>Onosmodium bejariense</i>	native	yes	p	forb
<i>Oxalis stricta</i>	native	no	p	forb
<i>Panicum capillare</i>	native	no	a	C <sub>4</sub>
<i>Panicum virgatum*</i>	native	yes	P	C <sub>4</sub>
<i>Pascopyrum smithii*</i>	native	yes	P	C <sub>3</sub>
<i>Paspalum setaceum</i>	native	yes	a	C <sub>4</sub>

<i>Penstemon digitalis</i> *	native	yes	p	forb
<i>Penstemon gracilis</i>	native	yes	p	forb
<i>Penstemon grandiflorus</i> *	native	yes	p	forb
<i>Physalis heterophylla</i>	native	no	p	forb
<i>Plantago patagonica</i> *	native	yes	a	forb
<i>Poa prattensis</i>	exotic	no	p	C <sub>3</sub>
<i>Potentilla norvegica</i>	native	yes	a	forb
<i>Prunella vulgaris</i>	native	yes	p	forb
<i>Pycnanthemum virginianum</i>	native	yes	p	forb
<i>Ratibida columnifera</i> *	native	yes	p	forb
<i>Rosa arkansana</i>	native	yes	p	forb (woody)
<i>Rudbeckia hirta</i>	native	yes	b	forb
<i>Rumex crispus</i>	exotic	no	p	forb
<i>Schizachyrium scoparium</i> *	native	yes	p	C <sub>4</sub>
<i>Senecio plattensis</i> *	native	yes	b	forb
<i>Setaria sp.</i>	exotic	no	a	C <sub>4</sub>
<i>Silphium integrifolium</i>	native	yes	p	forb
<i>Sisyrinchium campestre</i>	native	yes	p	forb
<i>Solanum nigrum</i>	exotic	no	a	forb
<i>Solidago canadensis</i>	native	no	p	forb
<i>Solidago gigantea</i> *	native	yes	p	forb
<i>Solidago missouriensis</i> *	native	yes	p	forb
<i>Sorghastrum nutans</i> *	native	yes	P	C <sub>4</sub>
<i>Spartina pectinata</i>	native	yes	p	C <sub>4</sub>
<i>Sporobolus compositus</i>	native	yes	p	C <sub>4</sub>
<i>Sporobolus asper</i> *	native	yes	p	C <sub>4</sub>

<i>Symphytotrichum ericoides*</i>	native	yes	p	Forb
<i>Symphytotrichum lanceolatum</i>	native	yes	p	Forb
<i>Symphytotrichum novae-angliae</i>	native	yes	p	Forb
<i>Taraxacum officinale</i>	exotic	no	p	forb
<i>Teucrium canadense</i>	native	yes	p	forb
<i>Tradescantia bracteata</i>	native	yes	p	forb
<i>Tradescantia occidentalis</i>	native	yes	p	forb
<i>Tridens flavus</i>	native	yes	p	C <sub>4</sub>
<i>Verbena hastata*</i>	native	yes	p	forb
<i>Verbena stricta*</i>	native	yes	p	forb
<i>Verbena urticifolia</i>	native	no	p	Forb
<i>Vernonia fasciculata</i>	native	yes	p	forb
<i>Vitis riparia</i>	native	no	p	forb (woody)

**Table B-2.** SAS outputs associated with Figure 3-1 grouped by figure panels

Panel A

Effect	Num DF	Den DF	F Value	Pr > F
density	1	17.6	6.26	0.0224
seedrichness	1	17	14.72	0.0013
density*seedrichness	1	17.6	0.61	0.4468
rainout	1	20	0.84	0.3715
rainout*density	1	20	0.57	0.4577
rainout*seedrichness	1	20	1.37	0.2556
rainout*density*seedrichness	1	20	0.12	0.7343
year	1	40	9.78	0.0033
density*year	1	40	0.04	0.8428
seedrichness*year	1	40	2.77	0.1040
density*seedrichness*year	1	40	0.22	0.6439
rainout*year	1	40	0.22	0.6439
rainout*density*year	1	40	3.72	0.0607
rainout*seedrichness*year	1	40	0.00	0.9473
rainout*density*seedrichness*year	1	40	4.26	0.0456

Panel B

Effect	Num DF	Den DF	F Value	Pr > F
Density	1	17.2	19.75	0.0003
Seedrichness	1	17	33.41	<.0001



density*seedrichness	1	17.2	0.21	0.6521
rainout	1	20	5.61	0.0280
rainout*density	1	20	3.42	0.0792
rainout*seedrichness	1	20	0.75	0.3969
rainout*density*seedrichness	1	20	0.22	0.6466
year	1	40	0.55	0.4641
density*year	1	40	1.67	0.2040
seedrichness*year	1	40	0.09	0.7640
density*seedrichness*year	1	40	1.83	0.1831
rainout*year	1	40	0.07	0.7996
rainout*density*year	1	40	0.00	0.9782
rainout*seedrichness*year	1	40	0.45	0.5064
rainout*density*seedrichness*year	1	40	0.32	0.5764

Panel C

Effect	Num DF	Den DF	F Value	Pr > F
Density	1	18.4	5.53	0.0300
Seedrichness	1	17	36.31	<.0001
density*seedrichness	1	18.4	1.74	0.1849
rainout	1	20	0.40	0.5350
rainout*density	1	20	0.28	0.6049
rainout*seedrichness	1	20	0.62	0.4396
rainout*density*seedrichness	1	20	0.43	0.5186
year	1	40	3.29	0.0773
density*year	1	40	1.07	0.3063
seedrichness*year	1	40	6.71	0.0133
density*seedrichness*year	1	40	1.68	0.2026
rainout*year	1	40	1.68	0.2026
rainout*density*year	1	40	2.42	0.1280
rainout*seedrichness*year	1	40	1.07	0.3063
rainout*density*seedrichness*year	1	40	3.29	0.0773

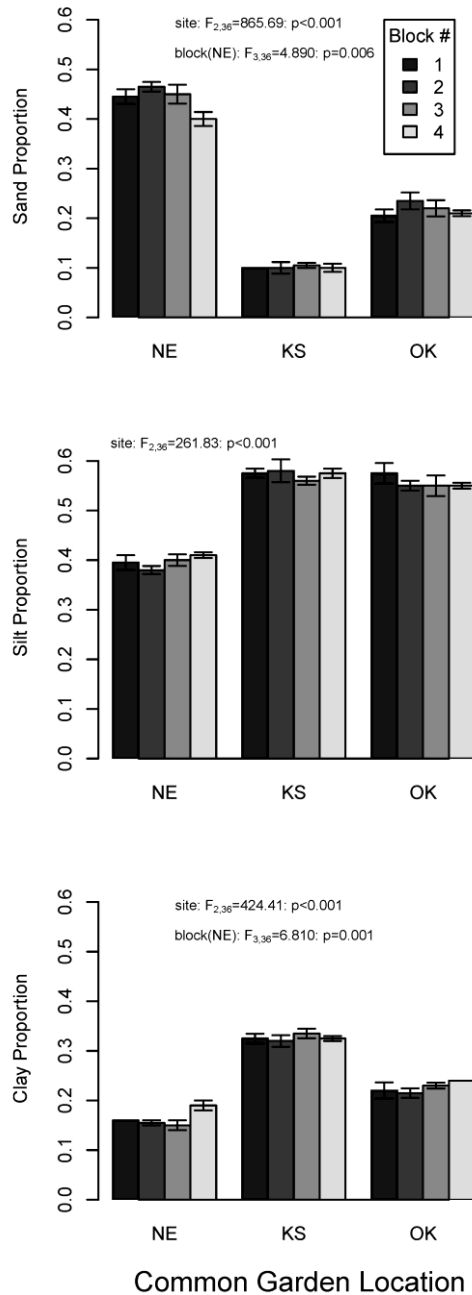
Panel D

Effect	Num DF	Den DF	F Value	Pr > F
seedrichness	1	37	14.75	0.0005
density	1	37.7	12.25	0.0012
density*seedrichness	1	37.7	1.60	0.2140
rainout	1	37	1.34	0.2546
rainout*seedrichness	1	37	0.27	0.6067
rainout*density	1	37	1.88	0.1790
rainout*density*seedrichness	1	37	0.16	0.6922
year	1	40	4.97	0.0315
seedrichness*year	1	40	2.48	0.1230
density*year	1	40	1.35	0.2529
density*seedrichness*year	1	40	0.08	0.7754
rainout*year	1	40	10.29	0.0026
rainout*seedrichness*year	1	40	0.05	0.8218
rainout*density*year	1	40	0.77	0.3859
rainout*density*seedrichness*year	1	40	1.10	0.3015

**Table B-3.** Least squares means for richness, density, and drought main effects in Figure 3-1.

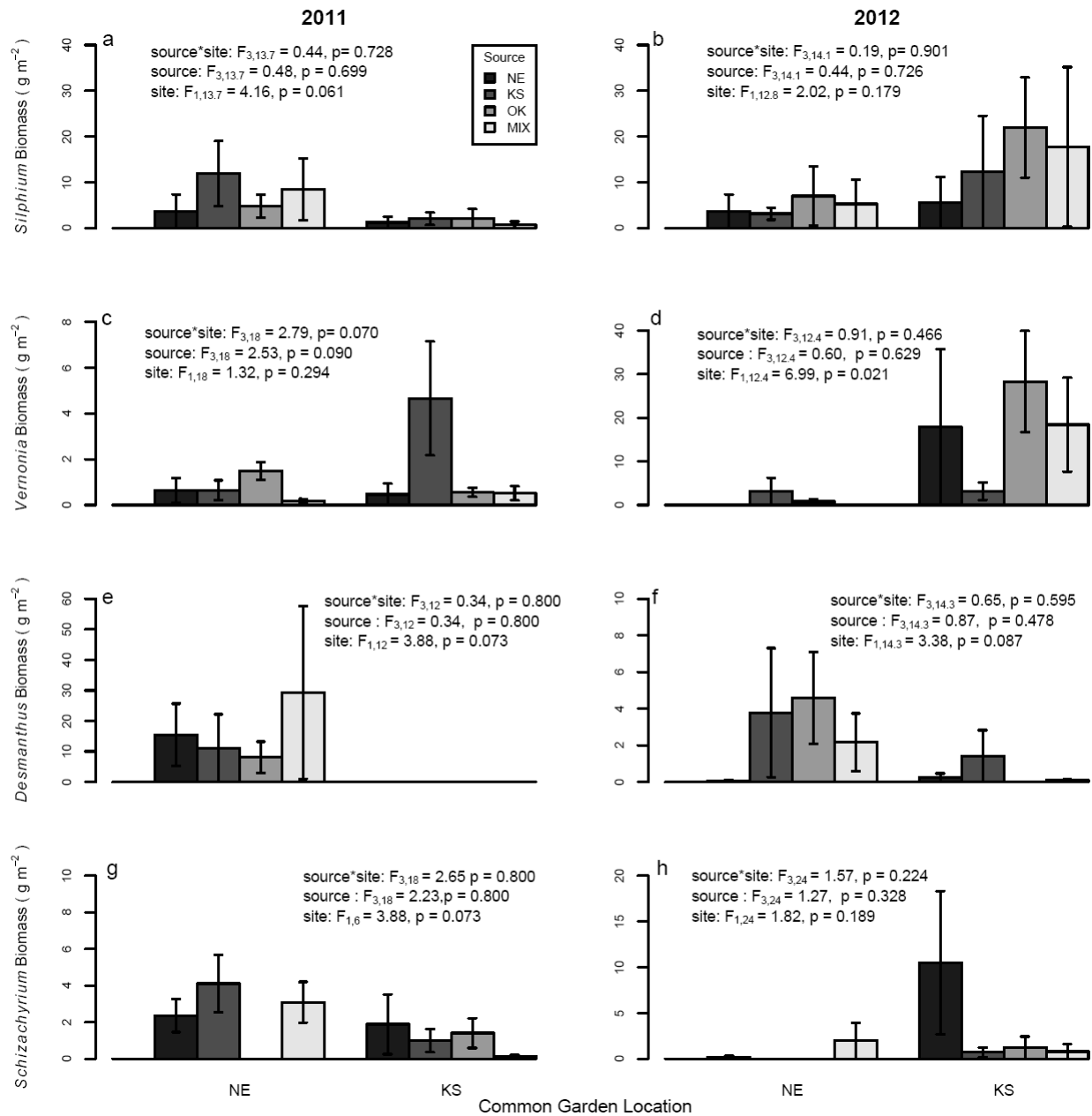
Response	HR	LR	HD	LD	Drought	No Drought
Seeded Richness	7.6	5.5	7.3	5.9	6.5	6.7
Seeded Cover	118.8	74.2	114.2	78.8	87.6	105.4
Exotic Richness	2.9	5.2	3.6	4.5	4.0	4.2
Exotic Cover	10.7	35.0	11.4	34.3	26.5	19.2

## Appendix C - Chapters 5 & 6: Site characteristics, seed mixture, and additional species from Chapter 5



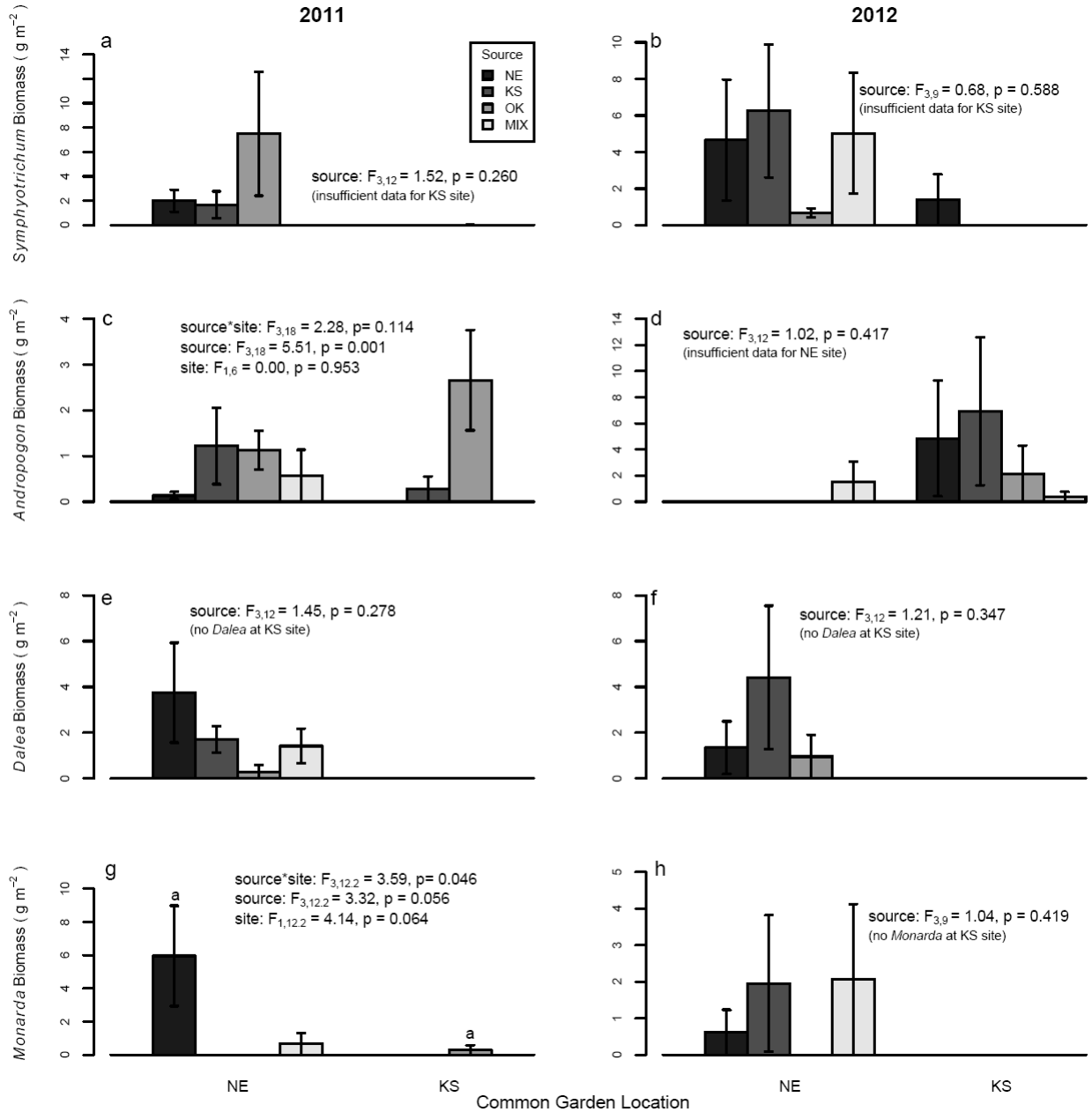
**Figure C-1.** Soil texture (sand, silt, and clay proportions) at the three common locations  $\pm$  1 S.E with statistics (F-statisticnum. df, den. df) for location and block(location) effects where

significant (Proc Mixed ANOVA). Two 10 cm deep, 2.54 cm diameter cores were taken near the center of each plot at each location in April-May, 2012. The two cores for each location were combined, dried, sieved, and sent to the Kansas State Agronomy Soil Testing lab for textural analysis.



**Figure C-2.** Aboveground biomass in 2011 (a, c, e, g) and 2012 (b, d, f, h) for the species with abundance (biomass) ranks 5-8 between common garden locations *Silphium*, *Vernonia*,

*Desmanthus*, and *Schizachyrium* (mean  $\pm$  1 s.e.m.). Statistics (F-statistic<sub>num. df, den. df</sub>) and significance are provided seed source, location and seed source  $\times$  location effects from Proc Mixed ANOVA.



**Figure C-3.** Aboveground biomass in 2011 (a, c, e, g) and 2012 (b, d, f, h) for the species with abundance (biomass) ranks 9-12 between common garden locations *Symphyotrichum*,

*Andropogon*, *Dalea*, and *Mondarda* (mean  $\pm$  1 s.e.m.). Statistics (F-statistic<sub>num. df, den. df</sub>) and significance are provided seed source, location and seed source  $\times$  location effects from Proc Mixed ANOVA where data were sufficient.

**Table C-1.** Site location, 1981-2010 mean and 2010, 2011, and 2012 observed total precipitation and temperature means for meteorological summer (June-August), and history for each common garden location.

Common garden location	1981-2010 mean ppt (mm), T (°C)	2010 observed ppt (mm), T (°C)	2011 observed ppt (mm), T (°C)	2012 observed ppt (mm), T (°C)	History
NE, Central Platte River Valley, 40° 44'N, 98° 35' W	272, 23	274, 24	318, 24	162, 25	agricultural land: corn
KS, Konza Prairie Biological Station, 39° 06' N, 96° 36' W	360, 25	142, 25	221, 27	268, 26	agricultural land: wheat/soy
OK, J.T. Nichol Preserve, 36° 04' N, 94° 49' W	342, 26	237, 27	109, 28	NA	agricultural land: wheat (wildlife plots)

Note: Weather station locations: NE = Hastings 4 mi N, Nebraska (40°39'N, 98°23' W); KS = Manhattan 6 mi SSW, Kansas (39°06'N, 96°37' W); OK = Tahlequah, Oklahoma (35°56N, 94°58W). We obtained climate online from the National Climatic Data Center (URL: <http://gis.ncdc.noaa.gov/map/cdo/>, accessed 12/16/2012) with the exception of observed conditions for OK, which were accessed online from Oklahoma Mesonet (URL: [http://www.mesonet.org/index.php/weather/category/past\\_data\\_files](http://www.mesonet.org/index.php/weather/category/past_data_files), accessed 12/16/2012).

**Table C-2.** Species in seed additions (nomenclature from United States Department of Agriculture Plants Database, URL: [plants.usda.gov/java](http://plants.usda.gov/java), Accessed 3/2012), amount of live seed added to each plot (equal among all seed sources), and broad functional groupings.

Species	Grams Live Seed / Plot (9m <sup>2</sup> )	Functional Group
<i>Achillea millefolium</i>	1.104	forb
<i>Andropogon gerardii</i>	21.760	C <sub>4</sub> grass
<i>Dalea candida</i>	0.878	legume
<i>Desmanthus illinoense</i>	10.293	legume
<i>Elymus canadensis</i>	10.900	C <sub>3</sub> grass
<i>Monarda fistulosa</i>	0.096	forb
<i>Oligoneuron rigidum</i>	8.068	forb
<i>Schizachyrium scoparium</i>	14.415	C <sub>4</sub> grass
<i>Silphium integrifolium</i>	10.718	forb
<i>Sorghastrum nutans</i>	36.279	C <sub>4</sub> grass
<i>Symphiotrichum ericoides</i>	0.398	Forb
Total	115.009	NA

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