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Plant community response to regional sources of dominant grasses in grasslands restored across a longitudinal gradient

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Abstract. Restorations in the light of climate change will need to take into account whether or not sources of the dominant plants are adapted to the future conditions at a site. In addition, the effect of these dominants, especially if sourced from outside the local area, on the assembling plant community needs assessment. We investigated how different ecotypes of the tallgrass prairie dominants *Andropogon gerardii* and *Sorghastrum nutans* affect assembling prairie communities. Four reciprocal common garden experiments were established across a longitudinal climate gradient characterized by a decrease in aridity in western Kansas (COLBY), central Kansas (HAYS), eastern Kansas (MANHATTAN), and southern Illinois (CARBONDALE). At each site, plots were seeded with ecotypes of *A. gerardii* and *S. nutans* sourced from central Kansas (CKS), eastern Kansas (EKS), southern Illinois (SIL), or a mix of all three regional ecotypes (MIX). All plots were also seeded with the same suite of seven subordinate species. Species composition was measured during the fourth year of restoration. The greatest variation between communities occurred at HAYS and CARBONDALE between plots seeded with CKS and SIL ecotypes. At these sites, plots seeded with the local source had the lowest diversity and cover of nondominant species. Compositional variation between plots seeded with different dominant grass ecotypes was found exclusively at CARBONDALE between CKS and SIL plots. Differences between locally seeded plots and plots seeded with a MIX of dominant grass ecotypes were contingent upon site. At CARBONDALE, MIX seeded plots had higher diversity than SIL ecotype plots. Our results indicate that across a wide geographic precipitation gradient, limited but important differences in community assembly occur in restorations established with different ecotypes of the dominant grasses. However, our results also support the use of mixtures of nonlocal ecotypes of dominant grasses in restorations without risk to the assembling plant community. Future studies need to determine the potential for out-breeding effects among seed sources in mixed stands.

Key words: *Andropogon gerardii*; community response; dominant species; ecotype; grassland; prairies; restoration; seed source; *Sorghastrum nutans*.

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INTRODUCTION

The loss of grasslands due to agricultural and urban development has made restoration efforts essential to preserve biodiversity and critical habitat for grassland species. Current restoration projects generally focus on use of locally collected seed in their plantings. Plants are considered to be adapted to the climatic, environmental and/or biotic conditions in which they grow. Use of a nonlocal seed source can put the success of a restoration at risk if genotypes that are not adapted

for growth in the planted environment are used (Vander Mijnsbrugge et al. 2010). Complicating the choice of seed source is that future climate change scenarios in temperate grasslands have predicted both increases and decreases in precipitation accompanying an increase in temperature (Craine et al. 2011, Intergovernmental Panel on Climate Change 2013). Therefore, sources adapted to the current climate may be maladapted to future conditions. One strategy for restoration practitioners to consider in future projects is the integration of nonlocal plant genotypes that may be adapted to the predicted future climatic conditions. Experimental testing of projected drier conditions can be accomplished through the use of rainout shelters (Yahdjian and Sala 2002, Aspinwall et al. 2013, Gherardi and Sala 2013, Vandegehuchte et al. 2015). Moreover, use of multiple intraspecific genotypes (i.e., a mixture of seed sources and ecotypes) would increase the genetic diversity of restored plant communities, resulting in a higher potential for adaptation and species survival in an uncertain future climate (Rice and Emery 2003) and potentially allowing increased subordinate species diversity (Gibson et al. 2012). The use of mixtures has been proposed as a suitable strategy for promoting community diversity and restoring disturbed sites (Lesica and Allendorf 1999).Before nonlocal seed is used in restoration plantings, it is important to understand potential impacts to the plant community. Understanding these effects is of particular importance for practitioners sourcing dominant grass species for restoration as the dominant species account for the majority of above-ground biomass in grassland ecosystems, reduce invasion by non-native species, and help to maintain ecosystem function (Smith and Knapp 2003, McCain et al. 2010, Wilsey 2010).

A prime example of a temperate grassland subject to intense restoration efforts in the face of extensive habitat loss and fragmentation is the North American tallgrass prairie. Originally extending over 677,300 km^2, this grassland has been reduced in extent by 96.8% (White et al. 2000). The dominant plants of the tallgrass prairie are C$_4$ grasses including *Andropogon gerardii* Vitman (big bluestem) and *Sorghastrum nutans* (L.) Nash (Indiangrass) contributing over 80% of vegetative cover in some areas (Weaver and Fitzpatrick 1934, Lauenroth et al. 1999). The wide range of

these dominant grasses has resulted in great variability in phenotypes between regional sources (McMillan 1959). Many species exist over a wide range of habitat types, growing under various biotic and abiotic conditions. These grasslands have been in place for the last 10,000 yr (Axelrod 1985) allowing adequate time for selection pressures to take place. It is not surprising, therefore, that adaptation to varied environments has resulted in diverging ecotypes within species as documented in other plant species (Turesson 1922, Clausen et al. 1941) and specifically in grasses (McMillan 1959, Lowry et al. 2014). Variation in ecotypes and phenotypes of dominant tallgrass prairie grasses, *Andropogon gerardii* and *Sorghastum nutans*, occurs across both north-south (McMillan 1959) and east-west gradients within their North American range (Gustafson et al. 1999, 2004, Olsen et al. 2013, Caudle et al. 2014, Gray et al. 2014). Studies of large-scale genetic similarity have shown that populations of *A. gerardii* within Illinois have significantly greater genetic similarity compared with populations in Arkansas and Kansas (Gustafson et al. 1999, Gray et al. 2014). *Sorghastrum nutans* showed a similar pattern with populations retaining the bulk of genetic variation and increases in geographic distance translating to greater genetic distance (Gustafson et al. 2004). These ecotypic differences among populations of both *A. gerardii* and *S. nutans* correspond to variations in performance and fecundity (McMillan 1959, Gibson et al. 2013b).

Although there has been research that shows genotypic (Gray et al. 2014) and phenotypic (Gibson et al. 2013b, Olsen et al. 2013) differences between regional sources of these dominant grass species are widespread, it is still unclear if: (1) regional ecotypes of dominant grasses *Andropogon gerardii* and *Sorghastrum nutans* differentially affect the assembling plant community, (2) how simulated drier climates would change the interaction of dominant grass ecotypes and the assembling community, and (3) if the use of high genotypic diversity of the dominant grass species in restoration plantings affects establishment and diversity of the plant community. The potential for the evolution of different ecotypes to affect community assembly has important eco-evolutionary implications (Shefferson and Salguero-Gómez 2015) related to how the genetic

structure of a dominant species can structure community dynamics (Bangert et al. 2008, Gibson et al. 2012).

This study focused on regional differences in *A. gerardii* and *S. nutans* from across the precipitation gradient from central Kansas to southern Illinois. Community composition was measured in the fourth year of a reciprocal, common garden transplant experiment to test the following hypotheses. First, increased productivity of *A. gerardii* has been linked with decreasing local plant diversity (McCain et al. 2010) and so it was predicted that diversity (richness and evenness) of the subordinate plant community would be lowest when associated with dominant grass ecotypes planted in their home environment and increase as grasses are collected further from their home environment. This "home site" hypothesis, reflects the observation that common garden experiments have shown that survival and productivity are negatively correlated with genetic and environmental distance from a "home site" (Montalvo and Ellstrand 2000, Kawecki and Ebert 2004, Bischoff et al. 2006). Second, it was predicted that experimental reduction in precipitation to mimic predicted increased aridity in the region would increase differences in diversity among the communities planted with different dominant grass ecotypes compared with under ambient conditions. By experimentally reducing rainfall, phenotypic differences in regional dominant grass ecotypes would increase resulting in greater differences in plant community diversity. Finally, it was predicted that subordinate species cover and diversity would be equal to or higher when grown with a mix of *A. gerardii* and *S. nutans* ecotypes as opposed to just the local ecotype. Ecological modeling has suggested that high levels of genetic diversity of dominant species (e.g., mixtures of ecotypes) can enhance niche availability and hence species richness of sub-ordinate species under conditions of relatively low environmental heterogeneity (such as in experimental plots) (Gibson et al. 2012).

METHODS

Site description

Common gardens were established in the spring of 2009 at four sites across a longitudinal gradient in the North American tallgrass prairie,

these sites include Colby, KS (COLBY), Hays, KS (HAYS), Manhattan, KS (MANHATTAN) and Carbondale, IL (CARBONDALE) (Fig. 1). From west to east across this gradient, there is a marked decrease in aridity (precipitation minus potential evapotranspiration) ranging from 97 in Colby, KS to −18 in Carbondale, IL and an increase in mean annual precipitation from 520 mm/yr in Colby, KS to 1201 mm/yr in Carbondale, IL based on 30 yr averages (Appendix S1: Fig. S1).

Experimental design

In the fall of 2008, seed of *Andropogon gerardii* Vitman was collected from remnant prairies within an 80 km radius of three of the common garden sites (HAYS, MANHATTAN, CARBONDALE). *Sorghastrum nutans* L. seed was collected from one local remnant prairie near each of the HAYS and MANHATTAN common gardens and from four remnants near the CARBONDALE common garden. Seeds of the nondominant species were purchased from a single commercial source (Appendix S1: Table S1). Seed was kept in dry storage before planting. The regional ecotypes of *A. gerardii* used in this study exhibit genetic and phenotypic differences (Gan et al. 2012, Zhang et al. 2012, Donatelli 2013, Gibson et al. 2013b, Olsen et al. 2013, Caudle et al. 2014, Gray et al. 2014). Populations of *A. gerardii* from Kansas have been shown to be genetically distinct from populations in southern Illinois (Gray et al. 2014). In addition, chemical differences between ecotypes of *A. gerardii* (Zhang et al. 2012, Caudle et al. 2014) have resulted in variability in forage quality (Donatelli 2013). Although reciprocal garden planting location plays a role in determining the magnitude of phenotypic differences between ecotypes, some variation between ecotypes remains regardless of planting location (Zhang et al. 2012, Donatelli 2013), providing evidence that these regional sources of *A. gerardii* are, in fact, genetically differentiated ecotypes. By contrast, the extent of ecotypic variation among the specific regional sources of *S. nutans* used in this study remains unknown, although based upon similar studies in the region (McMillan 1959, Gustafson et al. 2004), it is expected to be comparable to that of *A. gerardii*.
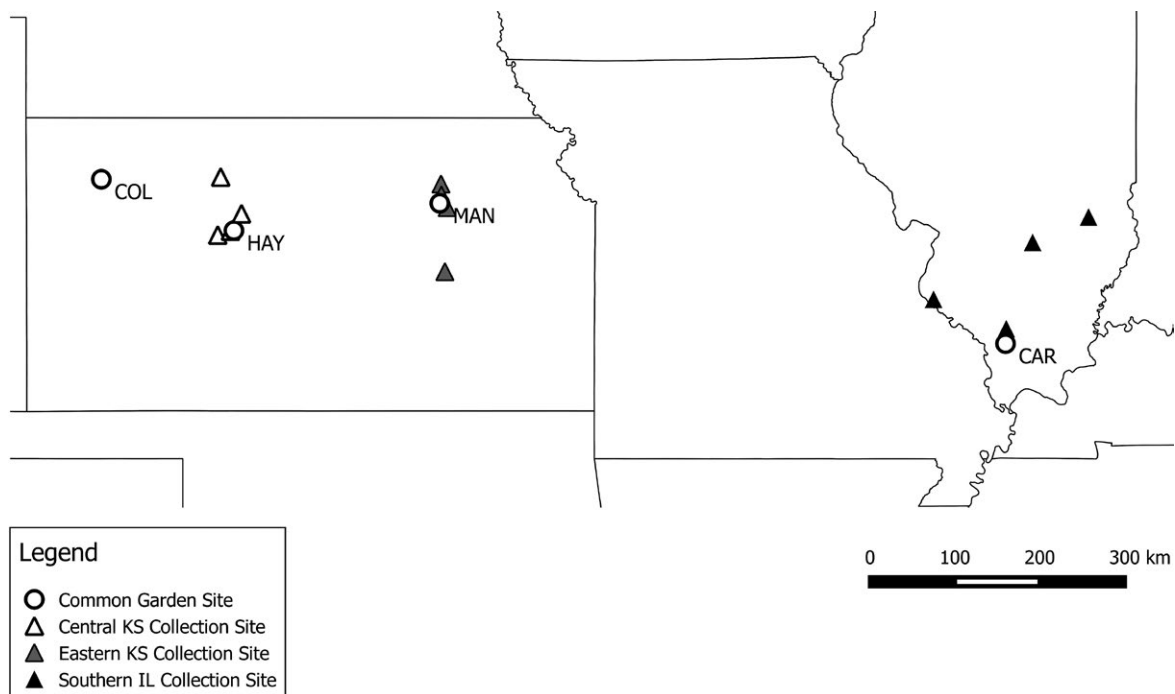
Fig. 1. Common garden locations and seed collection sites across the central North American Great Plains. COL = Colby, HAY = Hays, MAN = Manhattan, CAR = Carbondale. Full site details available in Johnson et al. (2015)

Common gardens were established according to a randomized complete block design at each of the four sites. The COLBY site was established as a satellite site to test the range of tolerance of *A. gerardii* and *S. nutans* under arid conditions. Each site contained four blocks of plots seeded with *A. gerardii* and *S. nutans* originating from three regions: central Kansas (CKS), eastern Kansas (EKS), and Illinois (SIL). Each block also contained a plot seeded with a mix of all three sources of these two grasses. At each site, plots seeded with mixed and locally collected seed were 4 m × 8 m. Plots planted with nonlocal seed were 4 m × 4 m. At COLBY, all plots seeded were 4 m × 4 m. The buffers between plots were seeded with *Bouteloua curtipendula* (Michx.) Torr. and *Schizachyrium scoparium* (Michx.) Nash purchased from a commercial supplier (Ion Exchange, Inc, Harpers Ferry, IA, USA).

In the spring of 2011, rainout shelters were constructed and placed over half of all except the mix-seeded plots in the HAYS, MANHATTAN, and CARBONDALE common garden sites. Shelters were constructed based on the design in Yahdjian

and Sala (2002). Shelters measure 2 m × 1.88 m with a roof of clear acrylic, V-shaped plates measuring 2 m long and 0.13 m wide spaced 20 cm apart. The roof of each shelter was angled to a 20° slope to ensure rain ran into a gutter placed on the low side and was guided away from the plots (Yahdjian and Sala 2002). The lowest side of the roof was 1.5 m above the ground surface to avoid interference with the plant canopy. In 2011 and 2012, rainout shelters were put up during late May to early June after 25% of growing degree days had accumulated at each site (earliest in MANHATTAN, latest in HAYS). These shelters are designed to intercept 50% of the precipitation (Yahdjian and Sala 2002), and reduced precipitation received under the shelters by 34–38% (determined from the amount of precipitation received and volume of intercepted water collected from the shelters following rain events in CARBONDALE from June through September 2012). This interception reduced soil moisture by 0%, 13%, and 19% in 2011 when the shelters were first installed, and in the year of study by 8%, 14%, and 25% relative to outside shelters in CARBONDALE, MANHATTAN,

and HAYS, respectively. Greater reduction in soil moisture under shelters from east to west can be attributed to the increasing aridity index across the gradient (CARBONDALE = −18; MANHATTAN = 41, HAYS = 81) (Wilson 2014).

Each field site was in crop production prior to establishing the reciprocal common garden experiment. Each field was lightly disked before seeding. All of the common gardens (excluding COLBY) were burned after the first growing season, either in the fall of 2009 or spring of 2010. Common garden sites were also burned in the spring or fall of 2011. COLBY was first burned in the spring of 2012.

During the 2012 growing season, all sites experienced a drought. From the months of April through October, the total precipitation in 2012 at CARBONDALE was 56% of the historic average based on 30 yr. At MANHATTAN, the precipitation between the same months in 2012 was 72% of the historic average. At HAYS, the precipitation during the 2012 growing season was 58% of the historic average and at COLBY the precipitation was 54% of the historic average (NOAA 2012) (Appendix S1: Fig. S1).

Species composition

Species composition was measured in four 1 m^2 quadrats per plot in which the percent canopy cover of each plant species rooted in the plot was estimated visually. In plots containing rainout shelters, two of the quadrats were placed under and two outside of the shelters. Species composition was estimated in the spring and fall of 2012, retaining the maximum value attained by each species from each survey date for analysis. The nomenclature used was according to the USDA Plants Database (Accessed 20 March 2013).

Hill's family of diversity numbers were used to describe diversity within each of the plots (Hill 1973). Hill's family of diversity numbers take into account three of the most important aspects of diversity, that is, total number of species (richness, Hill's N0), number of abundant species (Hill's N1 = exponent of Shannon's H' index) and the number of very abundant species (Hill's N2 = 1/Simpson's index = $1/\lambda$). These numbers estimate the "effective number of species" in a sample (Hill 1973) weighted by their individual abundances (Ludwig and Reynolds 1988).

Evenness was assessed using Alatalo's modified Hill's ratio. For this index, evenness (E) approaches zero as one species becomes more dominant within the community and approaches one when all species have equal abundances based on the equation

$$E = \frac{(1/\lambda) - 1}{e^{H'} - 1} = (N2 - 1)/(N1 - 1)$$

In the equation, λ, H', N1, and N2 are defined as in the calculation of Hill's diversity numbers (Alatalo 1981).

Statistical analyses

Plant cover from across the precipitation gradient was analyzed to determine if community composition and diversity varied based on planting location or dominant grass ecotype. All univariate procedures were completed in SAS® version 9 (SAS Institute Inc. 2002–2008). Within each site (CARBONDALE, MANHATTAN, and HAYS), cover and diversity of plants in CKS, EKS, and SIL ecotype plots and ambient and rainout treatments were compared using a mixed model, according to a split plot design to test for differences between ecotypes, rainout treatments and their interaction. Species cover and diversity in ambient treatments of the local ecotype plots (SIL in CARBONDALE, EKS in MANHATTAN, and CKS in HAYS) were compared with MIX plots using a mixed model two-way ANOVA. For COLBY data, all plots were compared using a mixed model ANOVA. Significance was set at $\alpha = 0.05$.

Community data were standardized by species maximum per plot and analyzed using nonmetric multidimensional scaling (NMDS) ordinations in DECODA with a Bray–Curtis dissimilarity matrix, 100 random starts, and 10,000 permutations for each site and for all sites combined (Minchin 1990). Stress values were evaluated to determine dimensionality, using a value of 0.20 as a cutoff for significance. Vectors of cover of dominant and nondominant species and diversity measures were fit to ordinations for individual sites (only vectors with a significant fit are presented below). Species centroid plots based upon species weighted averages were produced for those species with cover of 20% or more for the all-site comparison.
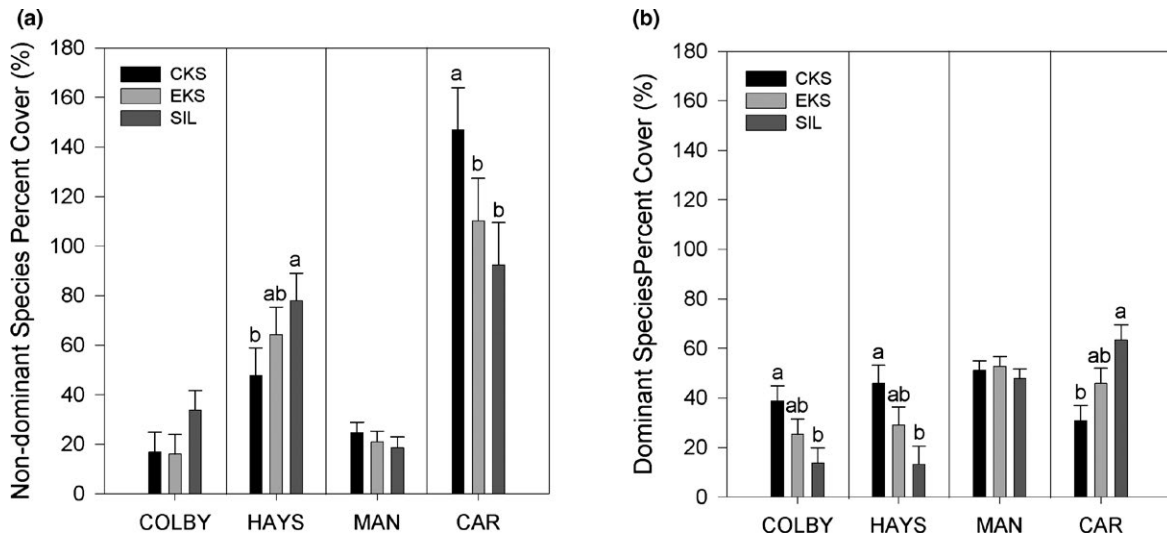
Fig. 2. The effects of dominant grass ecotype (CKS, EKS, and SIL) across COLBY, HAYS, MANHATTAN, and CARBONDALE sites (a) on nondominant species cover, and (b) on cover of dominant species (*Andropogon gerardii* and *Sorghastum nutans*). Values with the same letter above the bar were not significantly different ($\alpha > 0.05$). Insignificant comparisons ($\alpha > 0.05$) do not have letters above the bars.

Mixed model, permutational multivariate analysis of variance (PERMANOVA) and analysis of similarity (ANOSIM) were used to test for differences in composition between plots based upon Bray–Curtis dissimilarities with different ecotypes and treatments and completed in PRIMER v6 (Clarke and Gorley 2006). Block was treated as a random factor for all analyses.

Results

Site effects

The mean cover of dominant species was 44.4%±3.9%, 50.5%±1.7%, 28.7%±4.0, and 28.0% ±3.7% and the mean cover of nondominant species was 115.0%±7.8%, 20.9%±1.8%, 63.4% ±5.8%, and 20.8%±4.0%, at CARBONDALE, MANHATTAN, HAYS, and COLBY, respectively. *Sorghastrum nutans* was not present in any of the species composition sampling plots at COLBY, though it was seen at the site. The establishment and abundance of nondominant, sown species varied between sites. At CARBONDALE, HAYS, and COLBY, the cover of sown forbs accounted for 10–13% of all nondominant species. At MANHATTAN, sown forbs accounted for approximately 75% of all nondominant species.

Comparison of cover of nondominant and dominant species across all sites showed a pattern of community response to dominant grass cover (Fig. 2a,b). Generally, where dominant grass cover was highest, nondominant species cover was lowest and where dominant grass cover was lowest, nondominant species cover was highest. However, this inverse relationship was not significant at the COLBY site ($P > 0.05$). Across all sites, 84 unique species were identified with 64 at CARBONDALE, 30 at MANHATTAN, 23 at HAYS, and 19 at COLBY. All diversity values increased moving from west to east across the longitudinal gradient from COLBY to CARBONDALE (Fig. 3).

One-way ANOSIM results comparing species composition showed an overall difference between sites ($R = 0.76$, $P = 0.001$). A two-dimensional NMDS ordination (Stress = 0.20) showed clear separation between sites (Appendix S1: Fig. S2). Some overlap existed between plots from HAYS and MANHATTAN, although all pairwise comparisons showed significant differences between the composition at sites ($P = 0.001$ for all comparisons). A large number of volunteer forbs and one grass (*Setaria faberi* Herrm.) characterized plots at CARBONDALE (Appendix S1: Fig. S2). Communities at
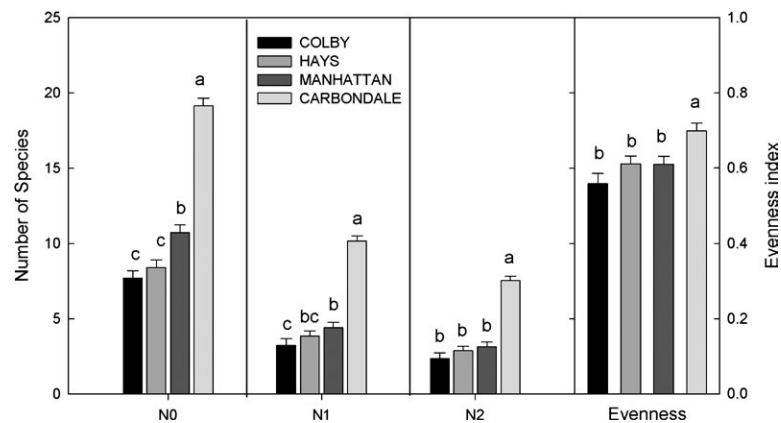
Fig. 3. Effects of site (COLBY, HAYS, MANHATTAN, and CARBONDALE) on plant community diversity. Diversity measures include N0 (richness), N1 (exponent of H′) and N2 (1/Simpson's index) diversity and evenness. Diversity values with the same letter above the bar were not significantly different ($\alpha > 0.05$).

MANHATTAN were characterized by the sown dominant *Sorghastrum nutans* (L.) Nash, and two sown forbs (*Monarda fistulosa* L. and *Asclepias tuberosa* L.). Plots at HAYS were characterized by an abundance of *Convolvulus arvensis* L. and *Bassia scoparia* (L.) A.J. Scott, as well as the sown forb *Penstemon digitalis* Nutt. ex Sims. The grasses, *Eleusine indica* (L.) Gaerth.(volunteer) and *Elymus canadensis* L. (sown), along with the volunteer forb *Tribulus terrestris* L., were found to be characteristic of communities at COLBY.

Comparisons of single ecotype plots and rainfall treatments

Ecotype source affected one or more aspects of species composition at each location. The rainfall treatment affected evenness at MANHATTAN and HAYS, but not CARBONDALE.

CARBONDALE.—There was a difference between ecotypes in the cover of dominant grasses and nondominant species (Table 1a). Plots with the SIL ecotype had higher cover of dominant grasses than plots with the CKS ecotype (Fig. 3b). Conversely, plots with the CKS ecotype had higher cover of nondominant species than plots with either EKS or SIL ecotypes. There was a significant effect of ecotype on Hill's N1, N2 and evenness values but not on N0 diversity at CARBONDALE (Table 2a). For all three variables, plots with the SIL ecotype had lower diversity than plots with CKS and EKS ecotype

(Fig. 4). There were no effects of rainout treatment on diversity values (Table 2a).

PERMANOVA analysis of species abundance data in ambient and rainout plots with CKS, EKS, and SIL ecotype showed significant block and ecotype × block effects (Table 3a). The greatest dissimilarity between ecotypes was in blocks 2 (CKS-EKS = 72%, CKS-SIL = 72%, EKS-SIL = 53%) and 4 (CKS-EKS = 81%, CKS-SIL = 82%, EKS-SIL = 70%). For blocks 1 and 3, all dissimilarities were under 70%.

One-way ANOSIM indicated an effect of ecotype on species composition between all plots when treatments were lumped ($R = 0.132$, $P = 0.024$). Pairwise comparisons indicated differences in species composition between plots with CKS and SIL ecotypes ($R = 0.18$, $P = 0.018$). A three-dimensional NMDS ordination (Stress = 0.17) showed that plots with the CKS ecotype were more dispersed than plots with EKS and SIL ecotypes (Fig. 5). Vector fitting analysis showed that cover of nondominant species increased along Axes 1 and 3, and decreased along Axis 2 (Table 4, Fig. 5).

MANHATTAN.—There were no effects of ecotype or ecotypes × rainout treatment on species cover (Table 1a, Fig. 2a), cover of dominant or nondominant species (Table 1a), or on any of the diversity values (Table 2a, Fig. 4). Pairwise ecotype × treatment comparisons showed ambient plots with the CKS ecotype and SIL ecotype with higher evenness than rainout

Table 1. F-values from a mixed model ANOVA, (a) on the effects of dominant grass ecotypes (CKS, EKS, or SIL), treatment (ambient or rainout) and the interaction on dominant and nondominant species cover by site, and (b) on the effects of a mix of all grass ecotypes vs. local ecotype plots (i.e., CKS in HAYS, EKS in MANHATTAN, and SIL in CARBONDALE) on species and functional group cover by site.

Site		df	Dominant species	Non-dominant species
(a)				
CARBONDALE	Ecotype (E)	2,15	$7.23_{2,18}$**	6.52**
	Treatment (T)	1,15	$0.56_{1,18}$	0.57
	T × E	2,15	$0.07_{2,18}$	0.54
MANHATTAN	Ecotype (E)	2,6	0.54	0.47
	Treatment (T)	1,9	2.48	0.70
	T × E	2,9	2.32	2.53
HAYS	Ecotype (E)	2,6	6.95*	$2.48_{2,15}$
	Treatment (T)	1,9	0.24	$0.22_{1,15}$
	T × E	2,9	1.01	$1.20_{2,15}$
COLBY	Ecotype	3,9	N/A	1.18
(b)				
CARBONDALE	Ecotype	1,3	9.95	0.42
MANHATTAN	Ecotype	1,3	1.77	0.01
HAYS	Ecotype	1,3	4.64	0.60
ALL	Ecotype	1,11	11.69**	0.98
	Site	2,11	2.10	18.87***

Notes: In (a) The COLBY site had no rainout treatment. Degrees of freedom are in subscript if they vary from the values given in the df column. In (b) Dominant grasses were not sourced from western Kansas (COLBY region) and no data are available for this comparison.

*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

Table 2. F-values from a mixed model ANOVA (a) on the effects of dominant grass seed ecotype (CKS, EKS, SIL), treatment (ambient or rainout), or the interaction on plant community diversity by site, and (b) on the effects of a mix of all grass ecotypes (MIX) and local ecotypes (i.e., CKS in HAYS, EKS in MANHATTAN, and SIL in CARBONDALE) on plant community diversity by site.

Site		df	N0	N1	N2	Evenness
(a)						
CARBONDALE	Ecotype (E)	2,15	1.45	6.27*	7.33**	8.92**
	Treatment (T)	1,15	0.04	0.01	0.06	0.47
	T × E	2,15	1.61	0.85	0.34	0.38
MANHATTAN	Ecotype (E)	2,9	$0.91_{2,15}$	0.00	0.03	0.27
	Treatment (T)	1,9	$1.79_{1,15}$	1.04	2.15	4.27
	T × S	2,9	$0.11_{2,15}$	1.53	2.98	4.15
HAYS	Ecotype (E)	2,6	$1.65_{2,9}$	0.60	0.32	$0.80_{2,15}$
	Treatment (T)	1,9	0.03	2.34	2.57	$13.07_{1,15}$**
	T × E	2,9	0.11	1.02	1.58	$4.03_{2,15}$*
COLBY	Ecotype	3,9	1.67	1.75	1.20	0.37
(b)						
CARBONDALE	Ecotype	1,3	31.78*	4.18	2.81	1.03
MANHATTAN	Ecotype	1,3	2.00	2.14	3.76	5.93
HAYS	Ecotype	1,3	1.59	1.64	2.44	4.19
MIX	Ecotype	1,11	10.31**	1.60	1.12	0.24
	Site	2,11	28.86***	16.59***	12.33**	0.62

Notes: In (a) the COLBY site has no rainout treatment. N0, N1, and N2 are Hill's (1973) diversity numbers. Evenness was calculated based on Hill's diversity numbers. Degrees of freedom are in subscript if they vary from the values given in the df column. In (b) Dominant grasses were not sourced from western Kansas (COLBY region) and no data are available for this comparison.
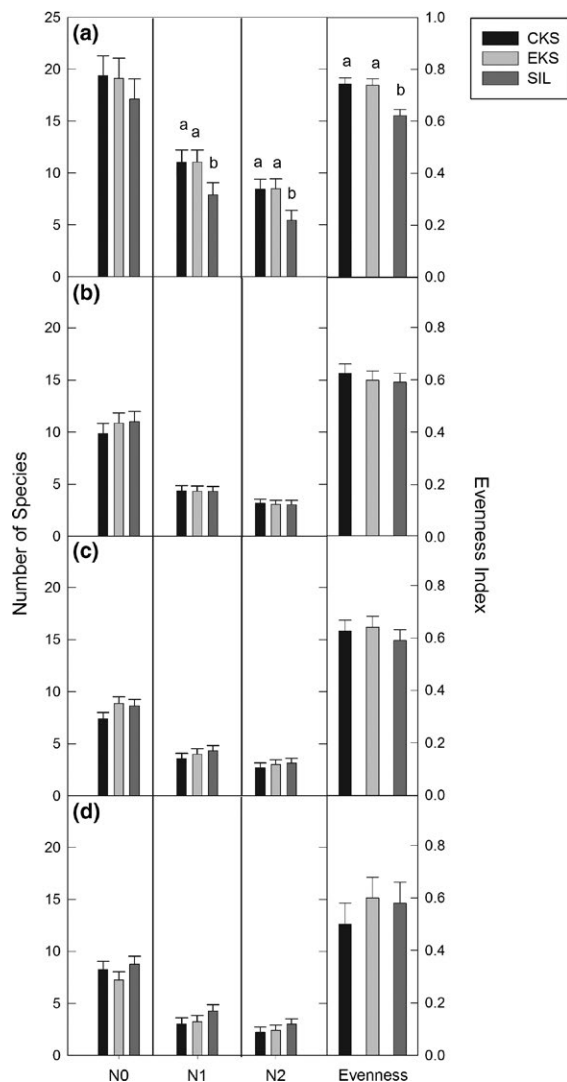
*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

Fig. 4.   The effects of dominant grass seed ecotype (CKS, EKS, or SIL) on diversity at (a) CARBONDALE, (b) MANHATTAN (c) HAYS, and (d) COLBY. Diversity measures include N0 (richness), N1 (exponent of H') and N2 (1/Simpson's index) diversity and evenness. Mean values among ecotypes and treatments with the same letter above the bar were not significantly different ($\alpha = 0.05$). Insignificant comparisons ($\alpha > 0.05$) do not have letters above the bars.

plots with the SIL ecotype ($t_{17.6} = 1.37$, $P = 0.02$ and $t_9 = 3.16$, $P = 0.01$, respectively).

Results from PERMANOVA tests between ambient and rainout plots with CKS, EKS, and

SIL ecotypes indicate a significant effect of block on species composition. There were no effects of either ecotype or rainout treatment, or any interaction (Table 3a). A two-dimensional NMDS ordination (Stress = 0.21) showed a scatter of plots based on dominant grass ecotype (Fig. 6: a 3-D solution with stress <0.2 was not of additional interpretative value). A one-way ANOSIM confirmed that there were no differences between different ecotype plots or between plots with rainout and ambient treatments ($R = -0.002$, $P = 0.398$). Vector fitting analysis showed significant trends in the cover of nondominant species and N0 diversity (Table 4). N0 diversity decreased along Axis 1 and decreased along Axis 2. The cover of nondominant species increased along Axis 2 decreased slightly along Axis 1.

HAYS.—In HAYS, there was a difference in dominant grass cover between plots with different ecotypes but not for cover of nondominant species (Table 1a). Pairwise tests indicated that plots with the CKS ecotype had higher cover of dominant grasses than plots with the SIL ecotype ($t_6 = 3.73$, $P = 0.01$) (Fig. 2b). There were no significant effects of dominant grass ecotype on the diversity of the plant community at this site (Table 2a, Fig. 4). There was an ecotype × rainout treatment effect on evenness (Table 2a). Pairwise comparisons showed higher evenness in the ambient plots with the CKS ecotype than in rainout plots with EKS and SIL ecotypes, and ambient plots with the SIL ecotype. Ambient plots with the EKS ecotype had higher evenness than rainout plots with CKS and EKS ecotypes.

PERMANOVA of species composition from ambient and rainout plots with CKS, EKS, and SIL ecotypes showed block and ecotype × block effects (Table 3a). Dissimilarity in species composition was greatest in block 4 (CKS-EKS = 52%, CKS-SIL = 76%, EKS-SIL = 71%). Plots with CKS and EKS ecotypes differed most in block 1 (70%) and block 3 showed the least dissimilarities between any of the plots (all values <60%). A two-dimensional NMDS ordination (Stress = 0.18) showed some separation of ecotypes, particularly plots with CKS and SIL ecotypes (Fig. 6b). Results of a one-way ANOSIM showed no significant differences in spe-

Table 3. Pseudo-F values from PERMANOVA (a) on the effects of dominant grass ecotype (CKS, EKS, or SIL), treatment (ambient or rainout), block (1–4) and the interactions on species composition (Bray–Curtis dissimilarities among plots) by site, and (b) on the effects of a mix of dominant grass ecotypes (CKS, EKS, and SIL) and the local ecotype (i.e., CKS in HAYS, EKS in MANHATTAN, and IL in CARBONDALE), as well as block (1–4) on species composition by site.

		Site			
	df	CARBONDALE	MANHATTAN	HAYS	COLBY
(a)					
Ecotype (E)	2,6	0.97	1.34	1.51	$0.74_{3,9}$
Treatment (T)	1,6	1.08	1.45	0.97	N/A
Block (B)	3,6	2.92**	3.30**	4.52**	$1.12_{3,9}$
E × T	2,6	0.91	1.10	1.51	N/A
E × B	6,6	2.50***	1.14	1.74*	N/A
T × B	3,6	0.89	1.27	1.06	N/A
(b)					
Ecotype (E)	1,3	1.39	1.00	1.49	N/A
Block (B)	3,3	1.17	1.12	1.31	N/A

Notes: Degrees of freedom are in subscript if they vary from the values given in the df column. In (b) dominant grasses were not sourced from western Kansas (COLBY region) and no data are available for this comparison (N/A). There was insufficient replication to run ecotype × block analyses.
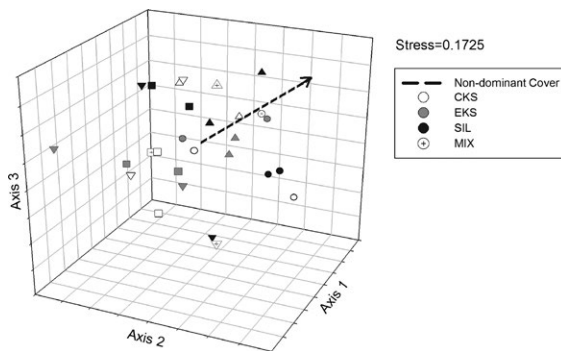
*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

Fig. 5. Three-dimensional NMDS ordination of species cover at the CARBONDALE site (Stress = 0.17) with significant vectors applied. Symbols represent population ecotypes of the dominant grasses, CKS = white, EKS = gray, SIL = black, and MIX = white with crosshairs. Shapes represent blocks, block 1 = circle, block 2 = upward triangle, block 3 = square, block 4 = downward triangle. The vector shows significant trends in the data with increasing values of nondominant cover in sites following in the direction of the arrow.

cies composition between ecotypes (R = 0.03, P = 0.30). The arrangement of plots in the ordination corresponded to vectors for the cover of nondominant species and dominant grasses, as well as N1 and N2 diversity and evenness (Table 4). The cover of nondominant species in-creased along Axis 1 and decreased along Axis 2 (Fig. 6b). All other variables decreased along Axis 1, and cover of dominant species increased along Axis 2. N1 and N2 diversity decreased along Axis 2.

COLBY.—In COLBY there was no significant difference in dominant grass cover between plots with different ecotypes (Table 2a). Pairwise comparisons showed plots with the CKS ecotype had higher cover of dominant grasses than plots with SIL ecotype (Fig. 2b). There was no effect of ecotype on nondominant species cover (Table 1a). There were no differences in community diversity among ecotypes (Table 2a).

There were no differences found in species composition between plots with different ecotypes at COLBY (Table 3a). A one-way ANOSIM also indicated that there were no differences between ecotypes (R = −0.132, P = 0.98). A two-dimensional NMDS ordination (Stress = 0.14) shows plots of various ecotypes tightly clustered with a number of outliers (Fig. 6c). N0, N1, and N2 diversity and evenness, but not cover of dominant or nondominant species, explains patterns in the ordination (Table 4). Evenness decreased along Axis 1 and increased along Axis 2 (Fig. 6c). N0, N1, and N2 diversity all increased along Axis 2 but N0 increased along Axis 1, whereas N1 and N2 decreased.

Table 4. Results of vector fitting analysis (R- and P-values) on the NMDS ordinations of species composition data.

| | Site | | | | | | | |
| | CARBONDALE | | MANHATTAN | | HAYS | | COLBY | |
Sample variable	R	P	R	P	R	P	R	P
N0	0.43	0.17	0.66	0.001***	0.26	0.41	0.70	0.015*
N1	0.19	0.83	0.31	0.29	0.49	0.03*	0.75	0.005**
N2	0.17	0.87	0.28	0.36	0.51	0.02*	0.76	0.004**
Evenness	0.13	0.94	0.34	0.20	0.57	0.007**	0.80	0.001***
Nondominant Cover	0.50	0.08	0.51	0.02*	0.80	<0.001***	0.57	0.16
Dominant Grass Cover	0.13	0.94	0.27	0.39	0.83	<0.001***	N/A	N/A

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

Comparison of mixed and single ecotype plots

There was no significant difference in the cover of dominant or nondominant species between plots with MIX and local (SIL) ecotypes (Table 1b) although at CARBONDALE plots with the SIL ecotype had higher cover of dominant grasses than plots with MIX ecotypes (67.6% ±8.4% and 30.3%±8.4%, respectively). There was a significant difference in N0 diversity comparing plots with SIL and MIX ecotypes at CARBONDALE (Table 2b) with N0 diversity in plots with the MIX ecotypes (N0 = 22.8 ± 1.8) being higher than in plots with the SIL ecotype (N0 = 16.5 ± 1.8). There were no effects of dominant grass ecotypes on N1 or N2 diversity or evenness at CARBONDALE, HAYS, or MANHATTAN. Comparison of ambient plots with the local ecotype (i.e., SIL at CARBONDALE, EKS at MANHATTAN, and CKS at HAYS) and plots with the MIX ecotypes showed no difference in species composition between ecotypes at any of the sites (Table 3b).

Discussion

Differences in regional ecotypes

The results of this study were consistent with the "home-site advantage hypothesis" (Montalvo and Ellstrand 2000). As the hypothesis predicts, plants grown in their "home site" performed better than those planted away from their home environment and thus, differentially affected the assembling plant community. This pattern became stronger as the environmental and geographic distance from the plants' home site increased (i.e., SIL plants in central and western KS and CKS plants at CARBONDALE).

Moreover, this pattern may be increasing in strength with restoration age as in 2010 and 2011 (the second and third years of the restoration), there was no detectable home-site advantage based on above-ground net primary productivity (ANPP) of the focal regional ecotypes of the dominant grasses in this study (Goad 2012, Johnson et al. 2015) although belowground effects of the ecotypes were evident by the third year of restoration (Mendola et al. 2015). In addition, in a related study, dominant grasses were not found to drive total ANPP early on in the restoration process (Baer et al. 2014). In the early years of a restoration, prairie communities are generally dominated by early-succession, weedy forbs. Perennial grasses begin to dominate the community only after the fourth year of the restoration (Baer et al. 2002, 2014, Gibson et al. 2013a). In this study, which was completed in the fourth year of the restoration, the dominant grasses accounted for 30–50% of the total cover across all plots and sites. Although ANPP was not considered as a part of this study, it is likely that productivity would have varied in a way consistent with the patterns found in dominant grass cover.

Contrary to our second prediction, the reduced rainfall treatment did not reveal variation in communities affected by the regional ecotypes of dominant grass. The extreme drought experienced in 2012 at all of the common garden sites could account for minimal significant results and suggests a degree of resilience of the restored communities to this level of drought. However, evenness of the plant community was lower under the rainout shelters compared with outside the rainout shelters in the Kansas sites
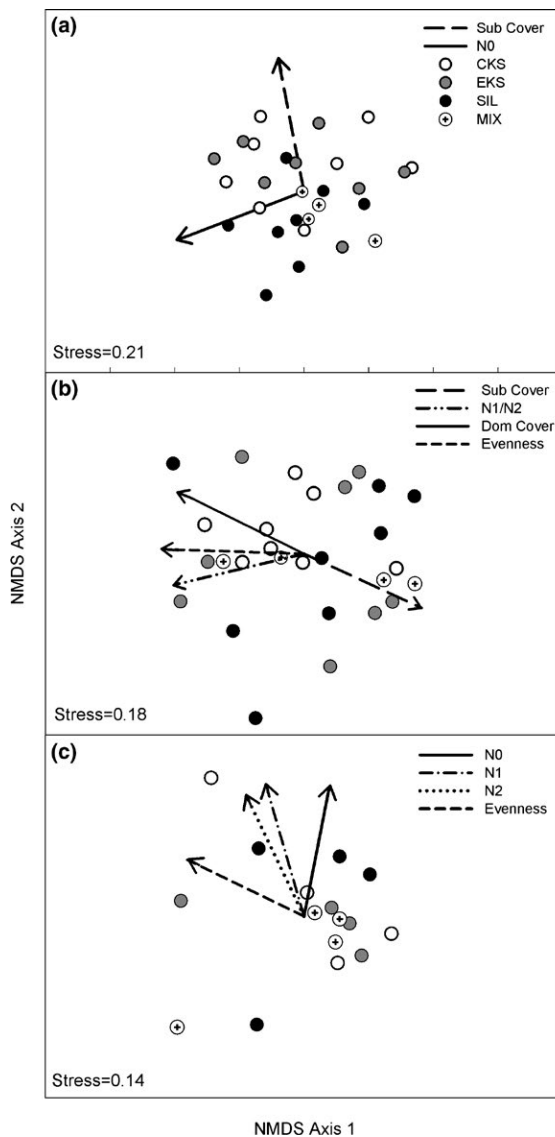
Fig. 6. Two-dimensional NMDS ordinations for (a) MANHATTAN data, (b) HAYS data, and (c) COLBY data. Symbols represent ecotypes of the dominant grasses, CKS = white, EKS = grey, SIL = black, and MIX = white with crosshairs. Vectors show significant trends in the data with increasing values following in the direction of the vector arrow (Sub-cover = cover of subordinate species; Dom-cover = cover of dominant species; N0, N1, and N2 = Hill's Diversity indices).

the communities at the more mesic (CARBON-DALE) end of the gradient. Forbs are more responsive to changes in precipitation than are C_4 grasses, such as *A. gerardii* and *S. nutans* (Knapp et al. 2001), which could account for this reduction in evenness. If climate change leads to increased drought as predicted under some models (Intergovernmental Panel on Climate Change 2013), then restoration resilience may depend upon geographic location and spatial scale as it appears to do in forest systems (Reyer et al. 2015).

Community response to diversity of ecotypes in dominant grasses

A challenge for current restoration projects is to create a community of species that will be able to thrive in the current climate but also to be preadapted to future conditions (Rice and Emery 2003, Ratajczak et al. 2014). Communities with high genetic diversity would have a higher potential for adaptation than those with only local genotypes when diversity within local populations is low (Rice and Emery 2003). In addition, climate change is predicted to reduce genotypic diversity of *A. gerardii* (Avolio et al. 2013). Although populations of *A. gerardii* have been shown to have higher genetic variation within populations, than among populations (Gustafson et al. 1999, 2004, Gray et al. 2014), this may not hold true under future climate conditions. With the use of non-local genotypes there is also a risk of out-breeding depression and fitness costs of subsequent generations (Edmands 2007). Future climates will not only be warmer but precipitation regimes are predicted to change dramatically (Craine et al. 2011, Avolio et al. 2013, Intergovernmental Panel on Climate Change 2013). There is some indication that stress, such as that brought on from rapid change in climate, limits out-breeding depression (Pederson 1968, Heschel et al. 2005). In cases where inbreeding depression is likely, the eminent loss of a population outweighs the cost of possible out-breeding depression (Edmands 2007, Hufford et al. 2012). Prior to the utilization of plantings with high genotypic diversity of dominant species in restorations, there is a need to determine their effects on the assembling plant community.

indicating that the subordinate communities at the naturally driest end of the longitudinal gradient studied were more susceptible than the dominant grasses to increased drought than

Consistent with our third prediction, this study showed that restoration practitioners can use a mix of regional ecotypes of dominant grasses while allowing the establishment in previously disturbed sites of a diverse assembling plant community. There was little difference in the cover of nondominant species between plots seeded with the local ecotypes and those with a mix of all regional ecotypes across the three sites. The use of seed mixes with high genetic diversity may also reduce the risk of invasion by exotic species. For example, some genotypes of *Solidago altissima* were found to be more effective at reducing invasion than others and thus, stands of higher genetic diversity of *S. altissima* had lower rates of invasion (Crutsinger et al. 2006). In general, native-dominated grasslands maintain higher diversity than exotic-dominated, grassland communities (Wilsey et al. 2009). In this study, plots sown with a mix of regional ecotypes generally had higher diversity than those planted with the local ecotypes, although the effects were highly dependent on planting location (found almost exclusively at CARBONDALE at the eastern, moist end of the tested precipitation gradient). Klopf et al. (2014) also found that some of the effects of dominant grass ecotypes on the surrounding plant community were regionally contingent; environmental variability between sites exacerbated differences between local dominant grasses and cultivars; and communities varied in response. The results of this study support inclusion of intraspecific variation in the filter model of community assembly (Gibson et al. 2012). It is likely that the nonlocal genotypes in the MIX plots were less adapted to the environmental conditions resulting in a decrease in their fitness and allowing for greater establishment of subordinate species, as the filter model suggests. There is also the risk when using genetically heterogeneous seed mixtures of outbreeding depression, maladaptation in plantings of mixed ecotypes, and intraspecific biotic homogenization (Crespi 2000, Kawecki and Ebert 2004, Olden et al. 2004, McKay et al. 2005). In plots containing only the local ecotypes, however, the dominant grasses were able to fill more niche space, presumably because they were highly adapted to their environment and, excluded more subordinate species.

CONCLUSION

This study tested the potential for different ecotypes of dominant grasses commonly planted in grassland restoration to determine the composition of the subordinate plant community. We found evidence to support the home-site advantage concept in experimental restoration plots after 4 yr of community development. However, the effect of ecotypes was contingent upon ecotype source and location of the restoration planting. Given the contingent effects of population source, restorationists should pay careful attention to ecotypic variation among dominant species. Mixed plantings of ecotypes can enhance diversity of the subordinate species community in some locations.

ACKNOWLEDGMENTS

LITERATURE CITED

Alatalo, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos 37:199–204.

Aspinwall, M. J., D. B. Lowry, S. H. Taylor, T. E. Juenger, C. V. Hawkes, M.-V. V. Johnson, J. R. Kiniry, and P. A. Fay. 2013. Genotypic variation in traits linked to climate and aboveground productivity in a widespread C4 grass: evidence for a functional trait syndrome. New Phytologist 199:966–980.

Avolio, M. L., J. M. Beaulieu, and M. D. Smith. 2013. Genetic diversity of a dominant C4 grass is altered with increased precipitation variability. Oecologia 171:571–581.

Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163–201.

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

Baer, S. G., D. J. Gibson, D. J. Gustafson, A. M. Benscoter, L. K. Reed, R. E. Campbell, R. P. Klopf, J. E. Willand, and B. R. Wodika. 2014. No effect of seed source on multiple aspects of ecosystem functioning during ecological restoration: cultivars

compared to local ecotypes of dominant grasses. Evolutionary Applications 7:323–335.

Bangert, R. K., E. V. Lonsdorf, G. M. Wimp, S. M. Shuster, D. Fischer, J. A. Schweitzer, G. J. Allan, J. K. Bailey, and T. G. Whitham. 2008. Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. Heredity 100:121–131.

Bischoff, A., et al. 2006. Detecting local adaptation in widespread grassland species – the importance of scale and local plant community. Journal of Ecology 94:1130–1142.

Caudle, K., L. Johnson, S. Baer, and B. Maricle. 2014. A comparison of seasonal foliar chlorophyll change among ecotypes and cultivars of *Andropogon gerardii* (Poaceae) by using nondestructive and destructive methods. Photosynthetica 52:511–518.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: user manual/tutorial. PRIMER-E Ltd, Plymouth, UK.

Clausen, J., D. D. Keck, and W. M. Heisey. 1941. Regional differentiation in plant species. American Naturalist 75:231–250.

Craine, J. M., J. B. Nippert, E. G. Towne, S. Tucker, S. W. Kembel, A. M. Skibbe, and K. K. McLauchlan. 2011. Functional consequences of climate change-induced plant species loss in a tallgrass prairie. Oecologia 165:1109–1117.

Crespi, B. J. 2000. The evolution of maladaptation. Heredity 84:623–629.

Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968.

Donatelli, J. 2013. Forage quality of *Andropogon gerardii* across a precipitation gradient. M.S. Thesis. Southern Illinois University, Carbondale, Illinois, USA.

Edmands, S. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology 16:463–475.

Gan, J., W. Yuan, L. Johnson, D. Wang, R. Nelson, and K. Zhang. 2012. Hydrothermal conversion of big bluestem for bio-oil production: the effect of ecotype and planting location. Bioresource Technology 116:413–420.

Gherardi, L. A., and O. E. Sala. 2013. Automated rainfall manipulation system: a reliable and inexpensive tool for ecologists. Ecosphere 4 (2):18.

Gibson, D. J., A. Allstadt, S. G. Baer, and M. Geisler. 2012. Incorporating the genetic diversity of foundation species into community assembly and diversity. Oikos 121:497–507.

Gibson, D. J., S. G. Baer, R. P. Klopf, L. K. Reed, B. Wodika, and J. Willand. 2013a. Limited effects of

dominant species population source on community composition during community assembly. Journal of Vegetation Science 24:429–440.

Gibson, D. J., G. Sendor, J. Donatelli, S. G. Baer, and L. Johnson. 2013b. Fitness among population sources of a dominant species (*Andropogon gerardii* Vitman) used in prairie restoration. Journal of the Torrey Botanical Society 140:269–279.

Goad, R. 2012. Response of regional sources of tallgrass prairie species to climate and soil microbial communities. M.S. Thesis. Southern Illinois University, Carbondale, Illinois, USA.

Gray, M. M., et al. 2014. Ecotypes of an ecologically dominant prairie grass (*Andropogon gerardii*) exhibit genetic divergence across the U.S. Midwest grasslands' environmental gradient. Molecular Ecology 23:6011–6028.

Gustafson, D. J., D. J. Gibson, and N. L. Nickrent. 1999. Random amplified polymorphic DNA variation among remnant big bluestem (*Andropogon gerardii* Vitman) populations from Arkansas' Grand Prairie. Molecular Ecology 8:1693–1701.

Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2004. Conservation genetics of two co-dominant grass species in an endangered grassland ecosystem. Journal of Applied Ecology 41:389–397.

Heschel, M. S., N. Hausmann, and J. Schmitt. 2005. Testing for stress-dependent inbreeding depression in *Impatiens capensis* (Balsaminaceae). American Journal of Botany 92:1322–1329.

Hill, M. O. 1973. Diversity and evenness – unifying notation and its consequences. Ecology 54:427–432.

Hufford, K. M., S. L. Krauss, and E. J. Veneklaas. 2012. Inbreeding and outbreeding depression in *Stylidium hispidum*: implications for mixing seed sources for ecological restoration. Ecology and Evolution 2:2262–2273.

Intergovernmental Panel on Climate Change. 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Johnson, L., J. T. Olsen, H. Tetreault, A. DeLaCruz, J. Bryant, T. J. Morgan, M. Knapp, N. M. Bello, S. G. Baer, and B. R. Maricle. 2015. Intraspecific variation of a dominant grass and local adaptation in reciprocal garden communities along a US Great Plains' precipitation gradient: implications for grassland restoration with climate change. Evolutionary Applications 8:705–723.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Klopf, R. P., S. G. Baer, and D. J. Gibson. 2014. Convergent and contingent community responses to grass

source and dominance during prairie restoration across a longitudinal gradient. Environmental Management 53:252–265.

Knapp, A. K., J. M. Briggs, and J. K. Koelliker. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. Ecosystems 4:19–28.

Lauenroth, W. K., I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystems in the central and north American grassland region. Great Plains Research 9:223–259.

Lesica, P., and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology 7:42–50.

Lowry, D. B., K. D. Behrman, P. Grabowski, G. P. Morris, J. R. Kiniry, and T. E. Juenger. 2014. Adaptations between ecotypes and along environmental gradients in *Panicum virgatum*. American Naturalist 183:682–692.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology. Wiley Interscience, New York, New York, USA.

McCain, K. N. S., S. G. Baer, J. M. Blair, and G. W. T. Wilson. 2010. Dominant grasses suppress local diversity in restored tallgrass prairie. Restoration Ecology 18:40–49.

McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local?" – A review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13:342–440.

McMillan, C. 1959. The role of ecotypic variation in the distribution of the Central Grassland of North America. Ecological Monographs 29:285–308.

Mendola, M. L., S. G. Baer, L. C. Johnson, and B. R. Maricle. 2015. The role of ecotypic variation and the environment on biomass and nitrogen in a dominant prairie grass. Ecology 96:2433–2445.

Minchin, P. 1990. DECODA – Database for Ecological Community Data, version 2.02. Research School of Pacific Studies, Canberra, Australia.

Montalvo, A. M., and N. C. Ellstrand. 2000. Transplantation of the subshrub *Lotus scoparius*: testing the home-site advantage hypothesis. Conservation Biology 14:1034–1045.

Olden, J. D., N. LeRoy Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19:18–24.

Olsen, J. T., K. L. Caudle, L. C. Johnson, S. G. Baer, and B. R. Maricle. 2013. Environmental and genetic variation in leaf anatomy among populations of *Andropogon gerardii* (Poaceae) along a precipitation gradient. American Journal of Botany 100:1957–1968.

Pederson, D. G. 1968. Environmental stress, heterozygote advantage and genotype-environment interaction in Arabidopsis. Heredity 23:127–138.

Ratajczak, Z., J. B. Nippert, J. M. Briggs, and J. M. Blair. 2014. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. Journal of Ecology 102:1374–1385.

Reyer, C. P. O., et al. 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of Ecology 103:5–15.

Rice, K. J., and N. C. Emery. 2003. Managing microevolution: restoration in the face of global change. Frontiers in Ecology and the Environment 1:469–478.

SAS Institute Inc. 2002–2008. The SAS System for Windows, version 9.2. SAS Institute Inc., Cary, North Carolina, USA.

Shefferson, R. P., and R. Salguero-Gómez. 2015. Eco-evolutionary dynamics in plants: interactive processes at overlapping time-scales and their implications. Journal of Ecology 103:789–797.

Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6:509–517.

Turesson, G. 1922. The species and variety as ecological units. Hereditas 3:100–113.

Vandegehuchte, M. L., Z. A. Sylvain, L. G. Reichmann, C. M. de Tomasel, U. N. Nielsen, D. H. Wall, and O. E. Sala. 2015. Responses of a desert nematode community to changes in water availability. Ecosphere 6(3):44.

Vander Mijnsbrugge, K., A. Brishoff, and B. Smith. 2010. A question of origin: where and how to collect seed for ecological restoration. Basic and Applied Ecology 11:300–311.

Weaver, J. E., and T. J. Fitzpatrick. 1934. The prairie. Ecological Monographs 4:113–295.

White, R., S. Murray, and M. Rohweder. 2000. Pilot analysis of global ecosystems: grassland ecosystems technical report. World Resources Institute, Washington, D.C., USA.

Wilsey, B. J. 2010. Productivity and subordinate species response to dominant grass species and seed source during restoration. Restoration Ecology 18:628–637.

Wilsey, B. J., T. B. Teaschner, P. P. Daneshgar, F. I. Isbell, and H. W. Polley. 2009. Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. Ecology Letters 12:432–442.

Wilson, L. R. 2014. Plant community response to regional sources of dominant grasses in grasslands

restored across a longitundinal gradient. M.S. Thesis. Southern Illinois University Carbondale, Carbondale, Illinois, USA.

Yahdjian, L., and O. E. Sala. 2002. A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133:95–101.

Zhang, K., L. Johnson, R. Nelson, W. Yuan, Z. Pei, and D. Wang. 2012. Chemical and elemental composition of big bluestem as affected by ecotype and planting location along the precipitation gradient of the Great Plains. Industrial Crops and Products 40:210–218.

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