Seed source has variable effects on species, communities, and ecosystem properties in grassland restorations

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Abstract.   Research to date regarding the relative advantages of local versus non-local sources of plant material for restoration has produced equivocal results. This research has typically focused on 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 under a range of environmental conditions using reciprocal common gardens at locations in three states (Nebraska, Kansas, and Oklahoma). In order to mimic the restoration of grassland vegetation under realistic conditions where multiple 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 establishment of individual species (measured as species-specific biomass), but responses were not consistent among species. No seed source had a consistent advantage across all sites or across all 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 only affected community structure 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 and primary 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.

Key words: common garden; community structure; dispersal; genetic diversity; local adaptation; managed relocation plant; productivity; provenance; restoration; seed transfer zone; tallgrass.

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INTRODUCTION

Phenotypes and genotypes of plant species vary across spatial and environmental gradients (Gustafson et al. 2004, Moncada et al. 2007, Weißhuhn et al. 2011). Such differences sometimes form the basis for recommending the use of locally sourced plant material when establishing, or restoring, native plant communities (Hamilton 2001, Miller et al. 2011), as do concerns regarding

the loss of local genetic diversity with the introduction of new genotypes (Wilkinson 2001, Hufford and Mazer 2003). However, the presence or direction of source effects can vary among species (Rice and Knapp 2008, Miller et al. 2011, Carter and Blair 2012), and there is little empirical support to date for the assumption that local sources provide a competitive advantage or enhanced restoration outcomes when multiple species are used (but see Weißhuhn et al. 2012). Variable and changing environmental conditions can also affect the relative success of different plant sources. This may be increasingly important, as anthropogenic climate change (Strzepek et al. 2010, Rahmstorf and Coumou 2011), nutrient deposition (Galloway et al. 2004), increases in atmospheric CO_2 (Hansen et al. 1981, O'ishi et al. 2009), and the presence of introduced producers and consumers (Walther et al. 2009, Burgiel and Muir 2010) continue to cause worldwide shifts from historical environments. Recognition of the many potential effects of such changes has increased debate regarding managed relocation (e.g., McDonald-Madden et al. 2011). Seastedt et al. (2008) also emphasize 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 (Ellstrand and Elam 1993, Keller and Waller 2002). 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 and Hamrick 1984). Where genetic variation is limited, increasing or changing available variation may improve or change responses to natural selection (Rice and Emery 2003). Harris et al. (2006) and Broadhurst et al. (2008) 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 establishment of individual species growing in mixed species communities, the combined aboveground productivity of all seeded species, and species richness and community structure. 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., Waser and Price 1985, Bischoff et al. 2006). 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 (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 most restoration projects involve the introduction of native vegetation representing several or many species (e.g., Cottam and Wilson 1966, Middleton et al. 2010). Despite this, we are aware of only a single study, which utilized a single common site, that simultaneously manipulated sources of multiple species and then evaluated species, community, and ecosystem responses concurrently (Weißhuhn et al. 2012). Filling this gap in knowledge is important, because individual species and/or community properties (e.g., richness or dominance) can affect productivity (Huston 1997, Smith and Knapp 2003, Fornara and Tilman 2009, Isbell et al. 2011). Fig. 1 presents a framework illustrating how single species responses might affect community and ecosystem properties (e.g., productivity). If seed source affects all species (circles, size representing species-specific biomass) the same way, it should also affect their combined productivity
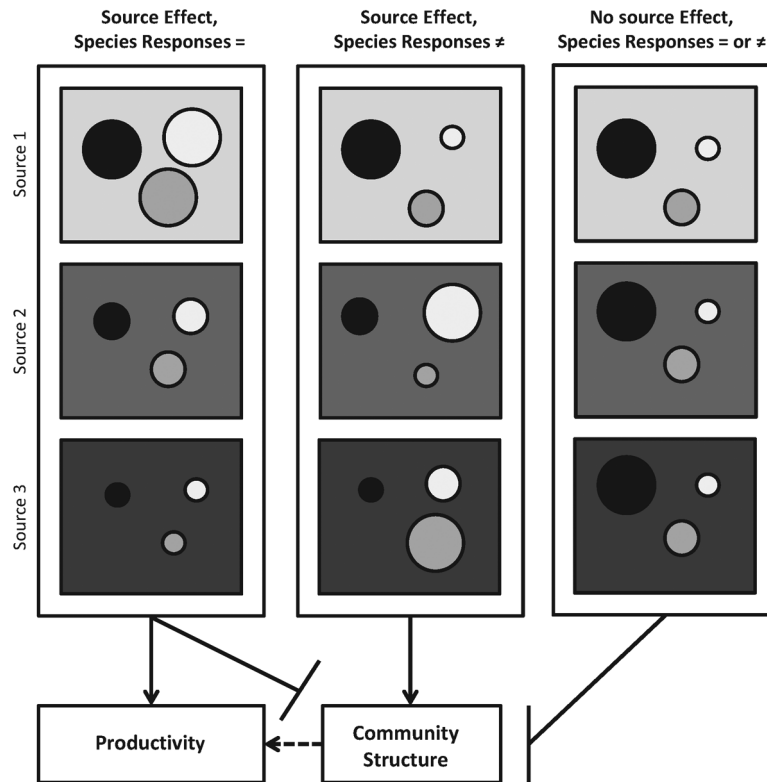
Fig. 1. Conceptual framework showing how individual species responses might affect productivity at one location (common garden). Solid arrows indicate effects, the dashed arrow represents potential effects, and intersecting solid lines indicate no effect. In the first column, similar species responses 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.

(first column, Fig. 1). However, productivity may also vary if seed source effects exist but exhibit different patterns among species (second column, Fig. 1), although the differential seed source effects among species could also offset one-another. For example, there may tend to be one species that performs very well in every seed source treatment, but the identity of that species may vary among treatments. Finally, if there is no effect of seed source on any species, then community structure and productivity should not differ among seed source treatments (third column, Fig. 1).

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 the 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 establishment 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 (Ehrenfeld 2001, Guo 2007). We predicted that because our 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 common garden locations. 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 (generally within 10 km, exceptions in Appendix B) 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 A for details).

Plots were 9×9 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 B 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 used were >20 m away from plots. Regeneration of native vegetation in tallgrass prairie is limited over periods of years or decades, even where remnant prairie is adjacent (Kindscher and Tieszen 1998).

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 during 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-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 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), perhaps due to drought (Appendix A). 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 16 randomly placed 0.25 m^2 quadrats (area 4 m^2) in each plot (plot area 9 m^2).

Data analysis

We used separate generalized linear mixed models in each year to test for differences in biomass for the 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, NC) 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 Development 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 × source interaction, we tested effects of source within individual locations.

Results

Individual species productivity

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 focused 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. 2).

Seed source effects on *Sorghastrum* biomass differed between locations in both years, and the KS source was consistently among the most productive (Fig. 2a–b). The OK source was more productive than the NE source at the NE location in both years (Fig. 2a–b), but the NE source was more productive than the OK source at the KS location in 2012 (Fig. 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. 2a–b).

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

Productivity for *Achillea* was greatest at the NE location in 2011 and greatest at the KS location in 2012 (Fig. 2e–f). There were no seed source effects on *Achillea* productivity (Fig. 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. 2g–h). The NE source was consistently among the most productive at the KS and NE locations in 2011 (Fig. 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. 2g–h).

Total seeded species productivity (ANPP)

The total aboveground productivity of combined seeded species differed among locations in 2010 and 2011with greater productivity at the NE location (Fig. 3a, b). However, seeded productivity was not significantly different between the KS and NE locations in 2012 (Fig. 3c). Seeded productivity did not significantly differ among source treatments in any year (Fig. 3).

Community properties

Species richness differed among locations in each year, but there were no significant effects of seed source on species richness (Fig. 4). Community structure differed among locations in 2011 and 2012 and differed among sources in 2011, but source effects on community structure in 2011 varied by location (Fig. 5). When analyzed within each common garden location, source effects remained significant (Adonis within locations: source$_{NE}$; $F_{3,15} = 2.25$, p = 0.005, source$_{KS}$; $F_{3,15} = 1.95$, p = 0.006). Generally, *Sorghastrum* was relatively more abundant than average at the KS common garden location, *Elymus* and *Oligoneuron* were relatively more abundant than average at the
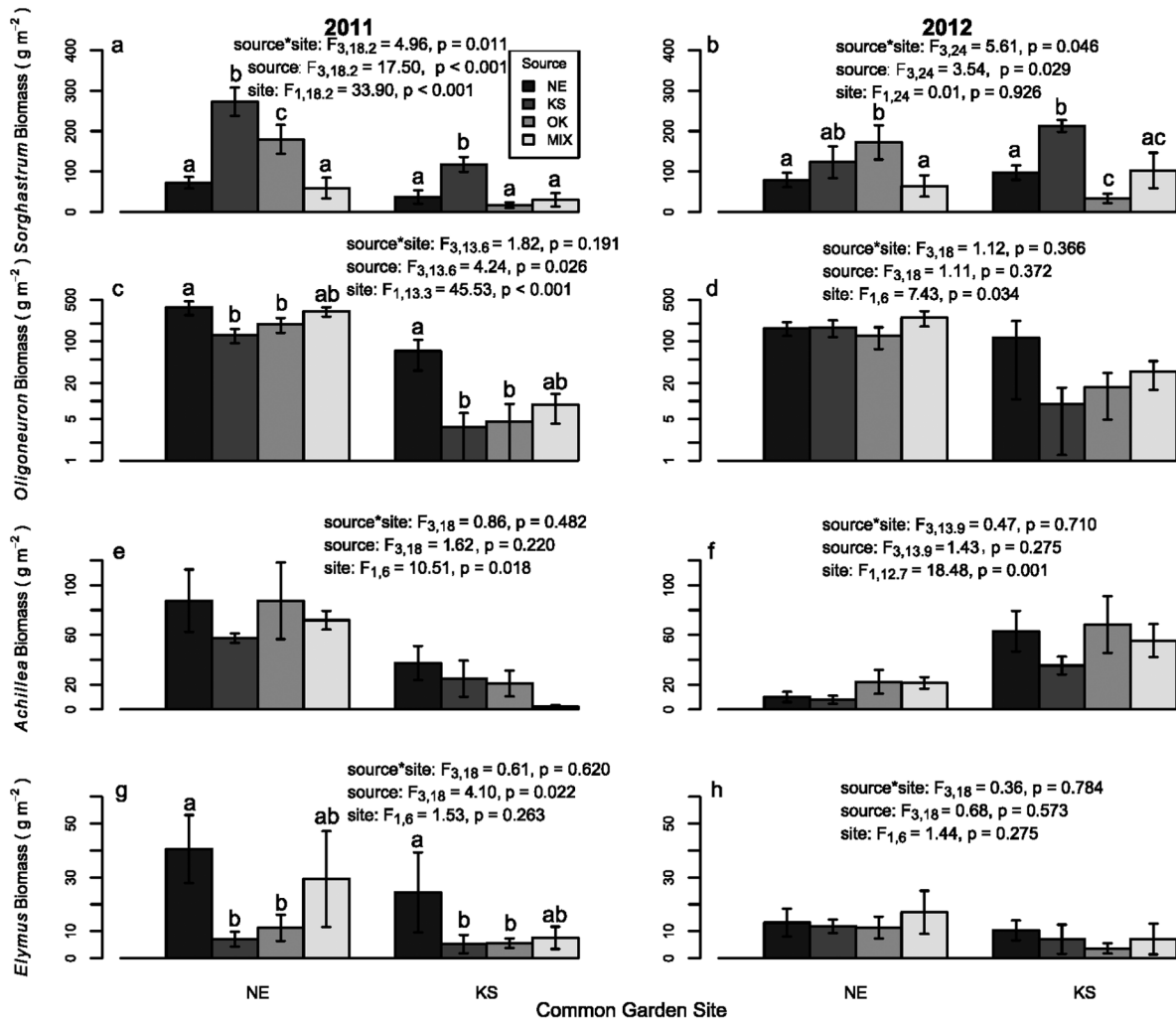
Fig. 2. Aboveground biomass from 2011 (a, c, e, g) and from 2012 (b, d, f, h) for the four most abundant species across years and common garden locations *Sorghastrum*, *Oligoneuron*, *Achillea*, and *Elymus* (mean ± 1 SE). Lower-case letters indicate significant differences among sources within locations (when the interaction p-value was ≤ 0.05) or among sources across locations (when the interaction p-value was > 0.05) after alpha adjustment (adjust = Tukey, SAS). Statistics (F-statistic, with degrees of freedom in subscript) and significance are provided for seed source, location and seed source × location effects from Proc Mixed ANOVA.

NE location, and the proportional representation of *Achillea* in communities in KS and NE differed among years (Fig. 5).

DISCUSSION

Our results do not indicate a general local advantage in terms of aboveground productivity of individual species or the total community, nor did source affect the richness of seeded species. Effects of source on community structure were detectable in 2011, but not 2012. Although there were some significant source effects on 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
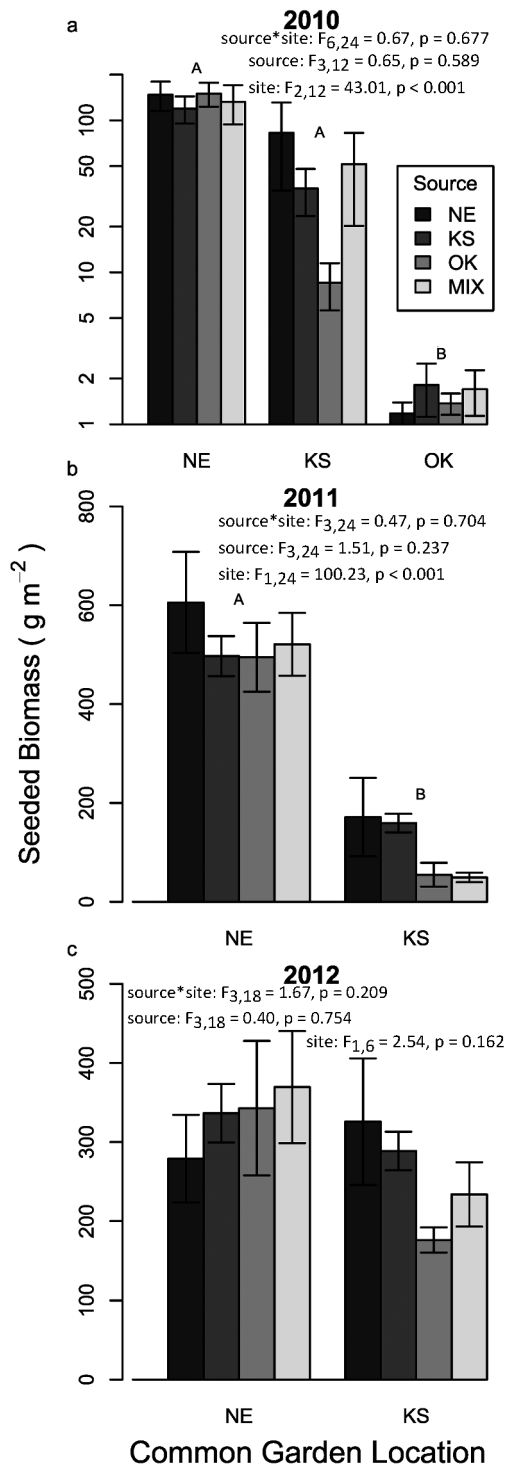
a

2010
source*site: $F_{6,24} = 0.67$, p = 0.677
source: $F_{3,12} = 0.65$, p = 0.589
site: $F_{2,12} = 43.01$, p < 0.001

A

A

Source
NE
KS
OK
MIX

B

NE   KS   OK

b

2011
source*site: $F_{3,24} = 0.47$, p = 0.704
source: $F_{3,24} = 1.51$, p = 0.237
site: $F_{1,24} = 100.23$, p < 0.001

A

B

Seeded Biomass (g m^{-2})

NE   KS

c

2012
source*site: $F_{3,18} = 1.67$, p = 0.209
source: $F_{3,18} = 0.40$, p = 0.754
site: $F_{1,6} = 2.54$, p = 0.162

NE   KS

Common Garden Location

Fig. 3. Total aboveground biomass for all seed species combined in (a) 2010, (b) 2011, and (c) 2012 (mean ± 1 SE). Upper-case letters indicate significant differences among locations. Statistics and significance follow Fig. 2.

for different species are not unique (Bischoff et al. 2006, Leimu and Fischer 2008, Hereford 2009, Weißhuhn et al. 2011), suggesting that the assumption of local advantage 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 A). 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., Hansen et al. 1981, Galloway et al. 2004). 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, Breed et al. 2013), 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 but not 2012 (Fig. 1). Productivity may not have significantly differed among sources, even in 2011 when community structure differed, because sources did not differ in terms of seeded species richness (Isbell et al. 2011). This may have maintained the possibility that a species with relatively high productivity could compensate for another with lower productivity (e.g., Yachi and Loreau 1999).

Differences in environmental conditions could 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 A). The productivity of C_4 grasses in Central Plains grasslands is positively associated with precipitation and soil sand content, but the productivity of C_3 grasses is negatively associated with soil sand content (Epstein et al. 1997*a*), and varies with temperature when precipitation effects are accounted for (Epstein et al. 1997*b*). Here, identical seed mixtures resulted in different community structures at different locations, which suggests that location environmental differences were important deter-
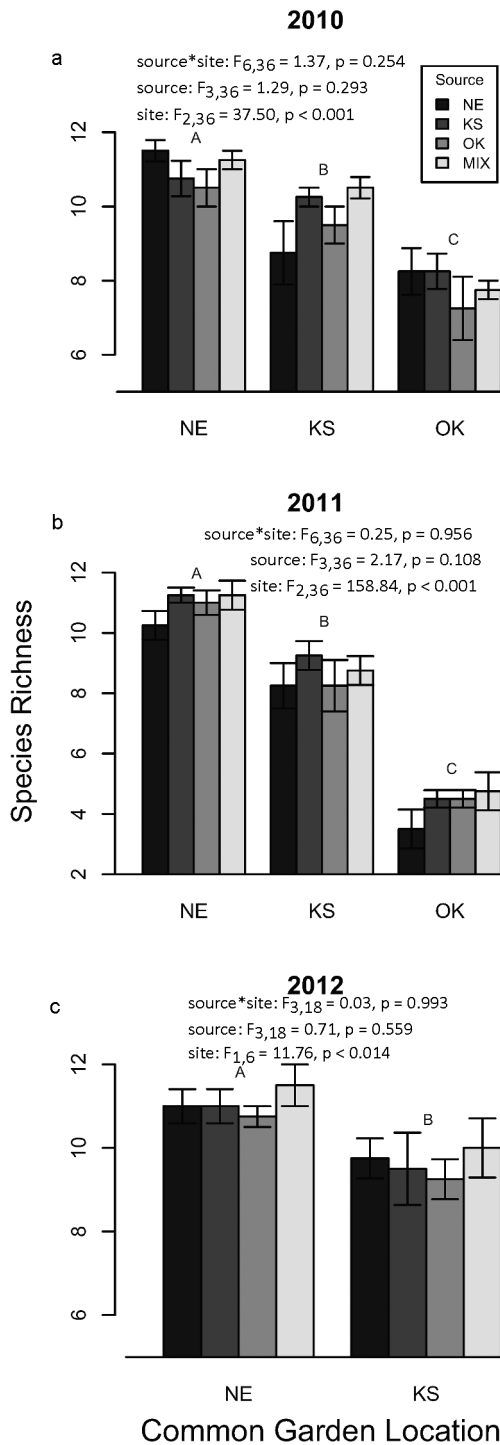
Fig. 4. Species richness in (a) 2010, (b) 2011, and (c) 2012 for all seeded species combined (mean ± 1 SE). Upper-case letters indicate significant differences among locations. Statistics and significance follow Fig. 2.

minants of community structure (e.g., Tilman 1997, Myers and Harms 2011). 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 and 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. 1). 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 establishment or combined productivity across variable locations

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 establish best (Fig. 2). Conversely, we may have found no source effects at all. This may, in part, explain why our conclusions differ from those of Weißhuhn et al. (2012), which were based on one common garden. 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,
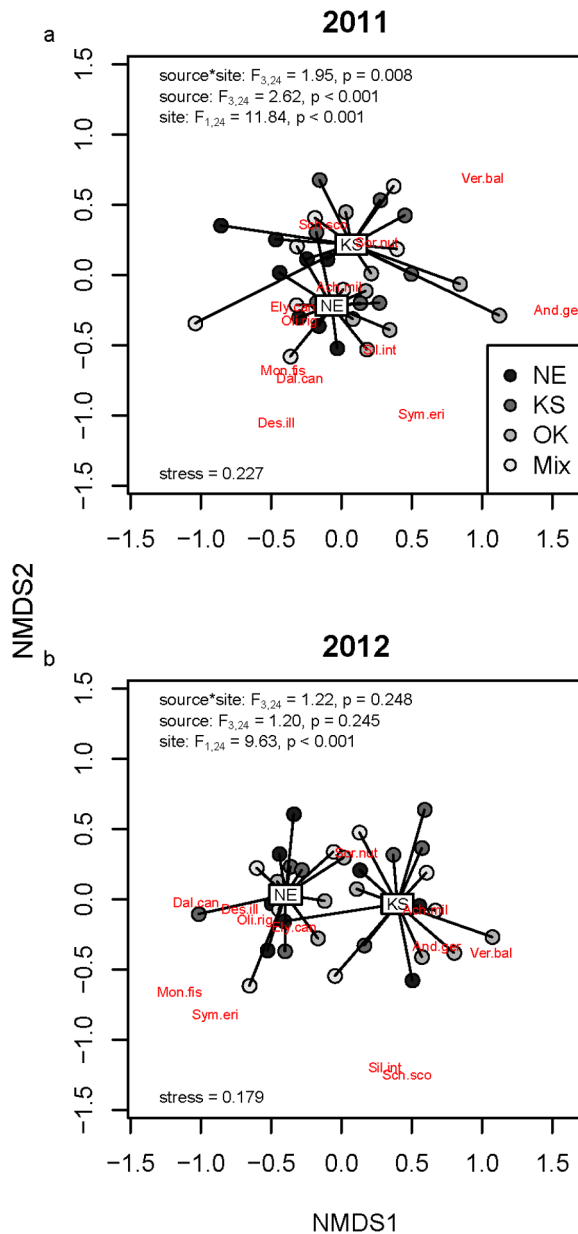
Fig. 5. Nonmetric multidimensional scaling (NMDS) ordinations for plant community structure with statistics from perMANOVA (R: "Adonis") and stress (statistics and significance follow Fig. 2). Lines connect points (different seed source treatments within common gardens) to common garden location. Species scores are provided as abbreviations (first three letters of genus and species). Species scores show the direction from the origin where larger than average abundances for species occur.

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. The prominence of year-to-year versus spatial variability in our study system (e.g., precipitation, Appendix A) may have reduced the development of local adaption (Kassen 2002, Kawecki and Ebert 2004). Alternatively natural selection may still act, or have acted in the past, to tune source populations to their local environments (Linhart and 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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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. 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		2010 observed		2011 observed		2012 observed		History
	Mean ppt (mm)	T (℃)	ppt (mm)	T (℃)	ppt (mm)	T (℃)	ppt (mm)	T (℃)	
NE	272	23	274	24	318	24	162	25	agricultural land: corn
KS	360	25	142	25	221	27	268	26	agricultural land: wheat/ soy
OK	342	26	237	27	109	28	NA	NA	agricultural land: wheat (wildlife plots)

Notes: Common locations: NE = Central Platte River Valley (40°44′ N, 98°35′ W), KS = Konza Prairie Biological Station (39°06′ N, 96°36′ W), OK = J.T. Nichol Preserve (36°04′ N, 94°49′ W). 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°56′ N, 94°58′ W). We obtained climate data 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, accessed 12/16/2012).
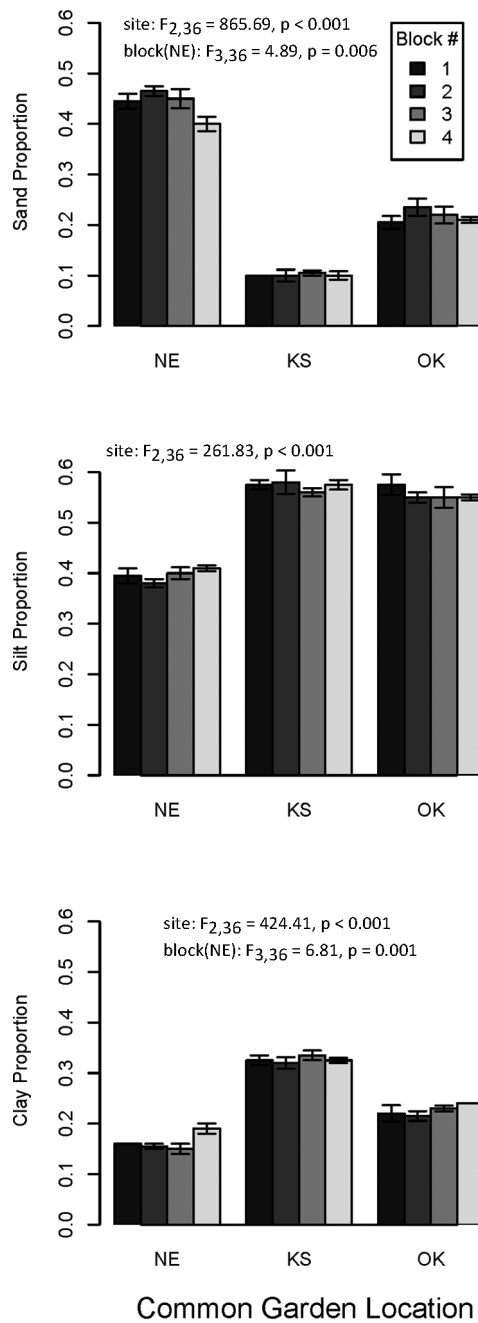
Fig. A1. Soil texture (sand, silt, and clay proportions) at the three common locations ± 1 SE with statistics (F-statistic, with degrees of freedom in subscript) for location and block(location) effects where significant (Proc Mixed ANOVA). Two 10 cm deep, 2.54 cm diameter cores were taken near the center 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.

Appendix B

Table B1. Seed weights for species sown into common garden plots. Species in seed additions (nomenclature from United States Department of Agriculture Plants Database, URL: plants.usda.gov/java, Accessed 3/2012), amount of live seed added to each plot (equal among all seed sources), and broad functional groupings. The OK sources for *D. illinoense* and *O. rigidum* were collected >10 km from the OK common garden location (64 km and 28 km, respectively).

| Species	Grams live seed/plot (9 m^2)	Functional group
Achillea millefolium	1.104	forb
Andropogon gerardii	21.760	C$_4$ grass
Dalea candida	0.878	legume
Desmanthus illinoense	10.293	legume
Elymus canadensis	10.900	C$_3$ grass
Monarda fistulosa	0.096	forb
Oligoneuron rigidum	8.068	forb
Schizachyrium scoparium	14.415	C$_4$ grass
Silphium integrifolium	10.718	forb
Sorghastrum nutans	36.279	C$_4$ grass
Symphiotrichum ericoides	0.398	Forb
Total	115.009	NA

Appendix C
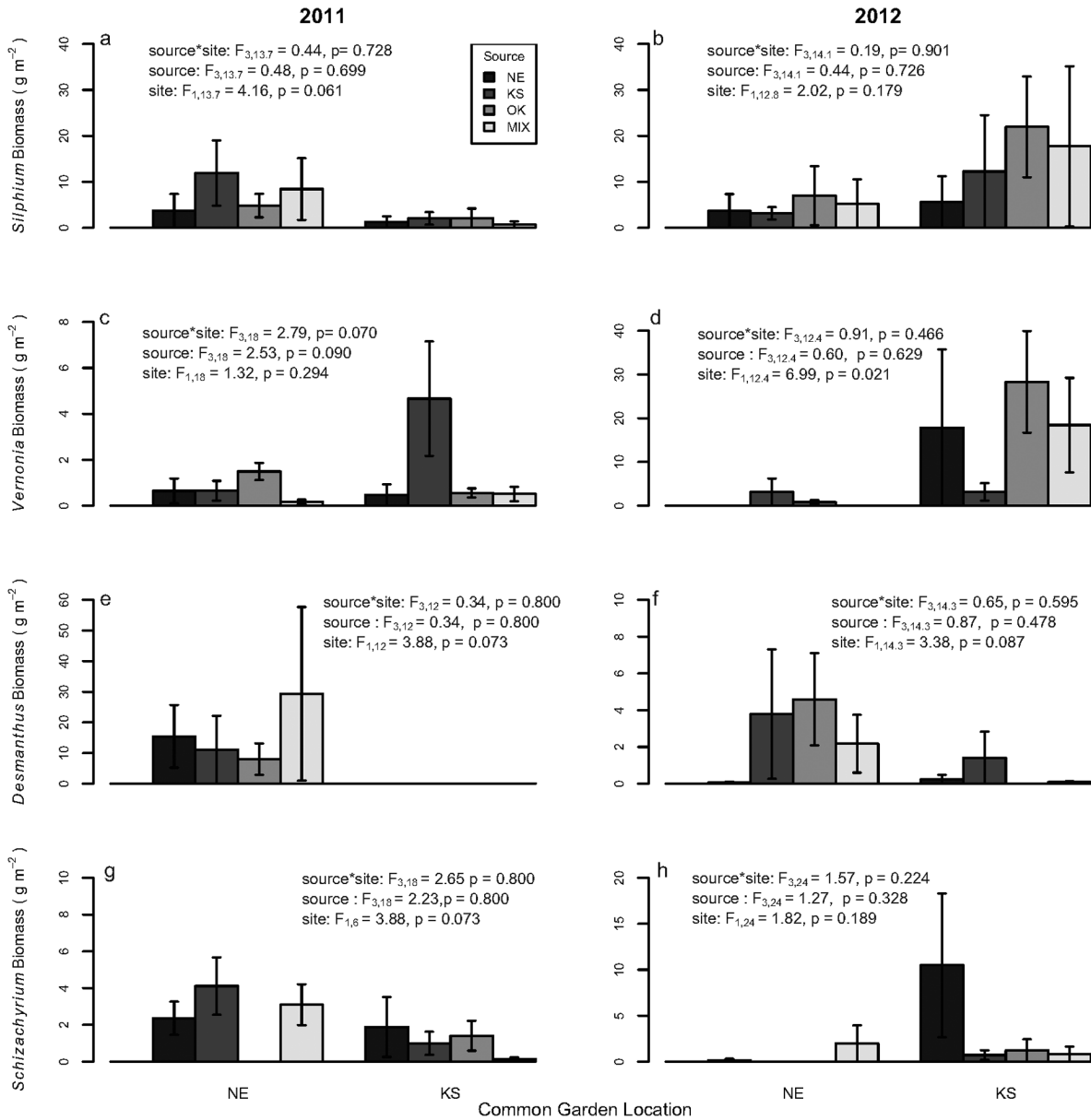
Fig. C1. Aboveground biomass in 2011 (a, c, e, g) and 2012 (b, d, f, h) for the species with abundance (biomass) ranks 5–8 between common garden locations: *Silphium*, *Vernonia*, *Desmanthus*, and *Schizachyrium* (mean ± 1 SE). Statistics (F-statistic, with degrees of freedom in subscript) and significance are provided for seed source, location and seed source × location effects from Proc Mixed ANOVA.
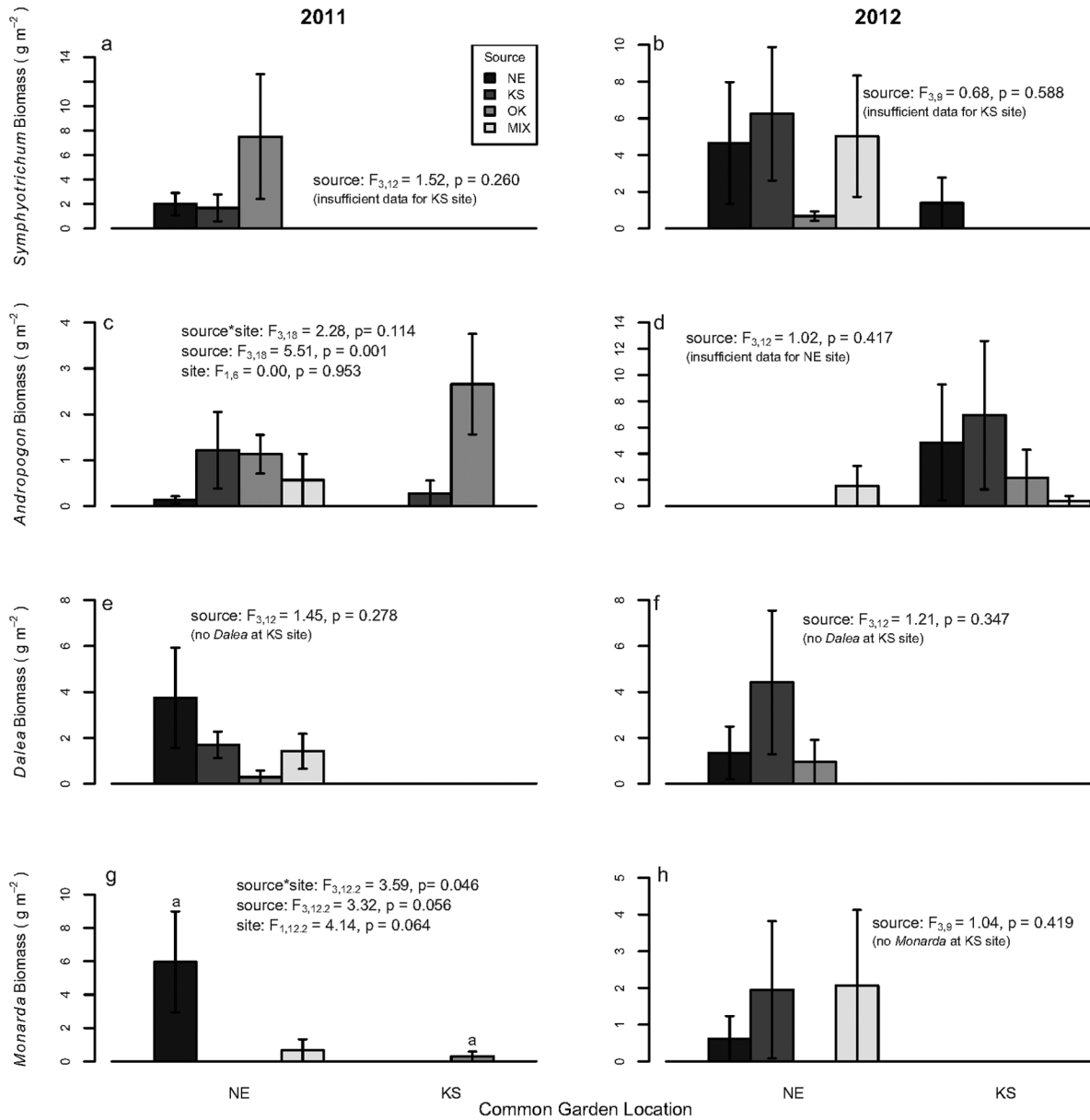
Fig. C2. Aboveground biomass in 2011 (a, c, e, g) and 2012 (b, d, f, h) for the species with abundance (biomass) ranks 9–12 between common garden locations: *Symphyotrichum*, *Andropogon*, *Dalea*, and *Mondarda* (mean ± 1 SE). Statistics (F-statistic, with degrees of freedom in subscript) and significance are provided for seed source, location and seed source × location effects from Proc Mixed ANOVA where data were sufficient.