

**PLANT PERFORMANCE IN PRAIRIE RESTORATIONS:
DOES SEED SOURCE MATTER?**

A THESIS SUBMITTED TO THE FACULTY OF THE PROGRAM IN PLANT BIOLOGY
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ABSTRACT

Restoration managers may select seed from a variety sources for their restoration projects. If the purchased seed is not of the local ecotype, land managers run the risk of poor establishment in the short-term and outcrossing between local and non-local ecotypes, genetic swamping, and the loss of local genetic diversity in the long-term. However, using seeds from local source populations may not be advantageous if local populations are inbred or maladapted to a changing environment. Moreover, purchasing non-local seed may be logistically and economically more practicable for most restoration projects than gathering seeds from local remnants. Although scientists have made great strides in addressing the potentially significant impact that seed source can have on restoration success, significant questions still remain.

In the present study, three warm-season prairie grass species from remnant, restoration, and nursery sources were planted as seeds and plugs into common garden sites located at three established prairie restorations in rural western Minnesota. The goals were to determine (i) the extent to which seed source influences germination and plant performance in established prairie restorations, (ii) whether germination and performance differ among restoration sites, and (iii) the difference between planting plugs and seeding directly seedling establishment and growth in restorations.

Seed source had a significant impact on seed germination and seedling performance in all three species during early establishment. Germination of *Andropogon gerardii* and *Bouteloua curtipendula* seeds from nursery and restoration sources were generally greater than remnant seeds. For example, *A. gerardii* nursery field-seedlings were more than double the size of remnant seedlings. In addition, seed performance differed among common garden sites, however

results were species specific. The effect of seed source on germination of *Sorghastrum nutans* seeds sown directly in the field varied among common garden sites, as evidenced by a significant interaction term ($p = 0.013$). Leaf length of plug-seedlings differed significantly among common garden sites for all species ($p < 0.0001$). Germination and survival was 3-6 times higher for plug-seedlings than for field-seedlings over the course of the experiment. However, once seedlings were established in the restoration sites, mortality was low in all three species, less than 1% for seeds planted in the field and 9-13% for plug-seedlings. Given concerns about founder effects and preserving local genetic variation, combined with the possibility that other long-term plant adaptations may exist that were not detected in this study, these results support the use of seed mixes from multiple local seed sources in enhancing short-term seedling establishment and success of prairie restorations.

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INTRODUCTION

Grasslands, especially in North America, have been highly impacted by habitat fragmentation and loss (Samson & Knopf, 1994; Gustafson et al., 2004a). Prior to European settlement, prairie was one of the largest ecosystems in North America, extending from Mexico north to Canada, and from the forest margins of Indiana and Wisconsin west to the Rockies, supporting a diversity of species and habitats (Weaver, 1954; Samson & Knopf, 1994). Conversion to row-crop agriculture reduced this once vast ecosystem from more than 160 million hectares to less than one percent of its former area (Samson & Knopf, 1994).

The near elimination of native prairie has inspired many efforts to protect remaining parcels and to create restored prairie areas (Schramm, 1990; Samson & Knopf, 1994; Lesica & Allendorf, 1999). The goal of most restoration projects is to reestablish historical ecosystem function by attempting to recreate the diverse, resilient, self-sustaining plant communities, which historically supported native biodiversity (Lesica & Allendorf, 1999). Much research has been devoted to understanding the complexities involved in restoring and maintaining ecosystem function and biological diversity in prairie habitats (Millar & Libby, 1989; Belnap, 1995; Lesica & Allendorf, 1999; McKay et al., 2005). Today, the importance of native species to local food webs and habitats, and the risks associated with introducing exotic, potentially invasive species are well understood (Lesica & Allendorf, 1999). However, the extent to which land managers should be concerned with the genetic composition of their source materials is not as well understood (Belnap, 1995; Lesica & Allendorf, 1999; McKay et al., 2005).

In recent years, conservation and restoration scientists have grappled with the question of seed source in restoration projects. On the one hand, there is a strong desire to conserve locally

adapted plants. Numerous studies have documented examples of adaptive genetic and morphological differentiation among plant populations (Gustafson et al., 2001; Joshi et al., 2001; Hufford & Mazer, 2003; Gustafson et al., 2004a; Gustafson et al., 2004b; Gustafson et al., 2005). Therefore, using seeds from local sources may maintain the genetic material best adapted to local conditions, thus increasing the potential success of the restoration project. In addition, studies have shown that the use of non-local seeds in restorations dilute genes associated with local adaptation and disrupt co-adapted gene complexes (Belnap, 1995; Lesica & Allendorf, 1999; Gustafson et al., 2001; Wilkinson, 2001; Hufford & Mazer, 2003; McKay et al., 2005; Kramer & Havens, 2009). Preservation of local adaptations may be crucial to the persistence of both the remnant and the restoration populations, and if non-local seeds are used, this advantage may be lost (Frankel & Soule, 1981; Millar & Libby, 1989; Lesica & Allendorf, 1999; Sackville Hamilton, 2001; Wilkinson, 2001). These considerations have led to the widespread support for the use of locally collected seed for restoration projects (Lesica & Allendorf, 1999; Sackville Hamilton, 2001; Hufford & Mazer, 2003; Kramer & Havens, 2009).

However, these considerations have been counterbalanced by another key concern of conservation and restoration ecologists: genetic diversity. The inability to adapt to changes in the environment is an important cause of extinction. The rate at which a population can evolve depends in part on its genetic variability (Sackville Hamilton, 2001; Gustafson et al., 2002; Dolan et al., 2008). Based on the theory that genetic variation is needed for long-term evolutionary change and short-term environmental adaptation, some have posited using non-local seed sources to provide new genetic material in areas where the local populations are depauperate or are poorly adapted to local conditions (Mills & Allendorf, 1996; Lesica &

Allendorf, 1999; Hufford & Mazer, 2003; McKay et al., 2005). In their 1999 review, Lesica and Allendorf discuss a number of molecular studies on grasses where investigators found little to no detectible genetic differentiation among populations in the study species despite their wide range and diverse habitats. Others have noted that populations of prairie grasses maintain multiple ploidy races that differ in ecological characteristics and that mixing these races may undermine restoration efforts (McKay et al., 2005; Soltis & al., 2007). In the absence of genetic differentiation or low genetic diversity, it may be unnecessary or even inadvisable to use local seed sources.

Concerns about preserving local adaptations, enhancing genetic diversity, and avoiding introgression of non-local genes into remnant populations have practical implications for land managers (Gustafson et al., 2005). In remnant systems, prairie grasses play a key role in regulating ecosystem function and native species diversity and suppressing invasive non-native species (Gustafson et al., 2004a; Middleton et al., 2010). Choosing the proper source of dominant prairie grasses for restorations is therefore a key component in the establishment a lasting, healthy ecosystem, both at the project site and in the surrounding native communities. Confronted with such an important decision, many practitioners seek guidelines for selecting populations within a species as seed sources for restoration efforts. Unfortunately, few guidelines exist for establishing self-sustaining, adapted populations (Hufford & Mazer, 2003; McKay et al., 2005).

A variety of potential seed sources often exists for prairie restorations, including seeds hand collected from local or non-local remnants, seeds propagated in fields from a mixture of local or non-local sources, and cultivar seeds. In Minnesota state law requires that, to the extent possible,

any restoration projects using state funds "plant vegetation or sow seed only of ecotypes native to Minnesota, and preferably of the local ecotype, using a high diversity of species originating from as close to the restoration site as possible, and protect existing native prairies from genetic contamination" (Minnesota Department of Natural Resources, 2009). The recommendation is to restrict collection for restoration, or for use in production fields, to within 240 km of the restoration project site, however areas as close to the project site as possible are preferred (Minnesota Department of Natural Resources, 2009). With thousands of acres in Minnesota being restored to native prairie each year by numerous state, federal, and private agencies, organizations, and citizens, restoration and management practices vary widely (Hier et al., 1999). Federal and state agencies collect the majority of their plant materials from within 160 km of restoration sites (Hier et al., 1999). However, much of the seed used for private restorations in Minnesota is purchased from native seed producers do not follow these guidelines. The native seeds sold by nurseries have their origins from remnant tallgrass prairie populations, but are rarely the actual hand-collected remnant seeds. Instead, the hand-collected seeds, often from multiple remnants, are planted in agricultural-type production fields and it is the offspring that are available for purchase. It is typical for these seed production lots to be located in a different county, sometimes a different state, than the actual remnants. Likewise, there is no guarantee that the original collection sites are local to any given restoration project.

While, there has been general support for collecting seeds locally, there has been little consensus on what exactly constitutes "local". Collecting within 8 km, 80 km, or even 300 km may not take into account environmental patchiness and habitat dissimilarities (Montalvo et al., 1997; Moncada et al., 2007). Indeed, distance may not be the best gauge of local adaptation,

especially in cases of environmental heterogeneity (Hufford & Mazer, 2003; Moncada et al., 2007). Moreover, for many restoration projects using locally collected seeds, either from one source or many, may be logistically and economically unrealistic (Lesica & Allendorf, 1999; McKay et al., 2005). These issues are of key importance for practitioners, but unfortunately, as of yet, scientists have been unable to provide any general guidelines from scientific theory or empirical studies.

In order to investigate the relationship between plant performance and seed source in prairie restoration, three dominant C4 grass species, *Andropogon gerardii* Vitman (Big Bluestem), *Sorghastrum nutans* (L.) Nash (Indiangrass), and *Bouteloua curtipendula* (Michx.) Torr. (Side-oats grama), were collected from local remnant (source ≤ 8 km), local restoration (source ≤ 80 km), and purchased from native nursery seed sources (source ≥ 160 km). Seeds from a total of 10 sources were planted either as plugs or directly as seeds into three existing restorations in rural western Minnesota. Individual seed germination and performance were tracked for all seeds during the first growing season. The overall purpose of was to determine (i) the extent to which seed source influences germination and plant performance in established prairie restorations, (ii) whether germination and performance differ among restoration sites, and (iii) the extent to which seedling establishment and growth in restorations differs between plants transplanted as plugs and those directly seeded.

MATERIALS AND METHODS

Study Species

Andropogon gerardii, *Sorghastrum nutans*, and *Bouteloua curtipendula* are dominant perennial warm-season (C4) grasses of the tallgrass prairie ecosystem (Weaver & Fitzpatrick,

1932). All three are self-incompatible polyploid species with a wide geographic distribution, including much of central and eastern United States, southern Canada, and parts of Mexico (Weaver, 1954; Sedivec et al., 2009). These species are used extensively in North American prairie restorations, as cover crops to reduce soil erosion and as native forage crops for livestock (Schramm, 1990; Wennerberg, 2006; Sedivec et al., 2009).

Andropogon gerardii is one of the co-dominant species of the tallgrass prairie system (Weaver & Fitzpatrick, 1932; Gustafson et al., 2004a). It is a rhizomatous, sod-forming grass in the tallgrass prairie and has a bunchgrass appearance in more arid regions (Wennerberg, 2006). *A. gerardii* is characterized by the blue coloration found at base of the culm, the distinct form of its inflorescences, typically composed of three (but up to seven) spike-like racemes, and the purplish, 3-parted flower clusters that resemble a turkey's foot (Wennerberg, 2006; Sedivec et al., 2009). A tall-statured grass, *A. gerardii* culms can reach up to 3 meters in height (Gleason & Cronquist, 1991). *Andropogon gerardii* begins growth in mid-May, and flowers between mid-July and mid-October (Wennerberg, 2006; Sedivec et al., 2009).

Sorghastrum nutans is the other co-dominant species of the prairie (Weaver & Fitzpatrick, 1932; Gustafson et al., 2004a). It is a deep-rooted bunchgrass, with dense, golden, plume-like seed heads (Gleason & Cronquist, 1991; Sedivec et al., 2009). Plants reproduce either sexually from seed or clonally from short, scaly rhizomes, and begin growth in mid-May, and can reach up to 2.5 meters in height (Gleason & Cronquist, 1991; Sedivec et al., 2009). Flowering occurs from late July to mid-October (Sedivec et al., 2009).

Bouteloua curtipendula is a common, sometimes dominant or co-dominant, species in the tallgrass prairie. *B. curtipendula* is a mid-height grass, with culms growing between 0.4-0.9

meters tall (Gleason & Cronquist, 1991). It has a distinctive inflorescence, consisting of a zigzag stalk with numerous small compressed spikelets that dangle from one side of the stalk at even intervals, hence the common name: side-oats grama (Gleason & Cronquist, 1991; Wynia, 2007; Sedivec et al., 2009). Culms have a bluish-green color, sometimes with a purplish cast (especially in the spring), which cures to a reddish-brown or straw color. It is a deep-rooted grass, which spreads very slowly by means of extremely short, stout rhizomes or reproduces sexually from seed (Gleason & Cronquist, 1991; Wynia, 2007). In the vegetative state, the grass is easily recognized by the long, evenly spaced hairs attached to the margins of the leaf ear at its base. Plants begin growth in mid-May, and flower between mid-July and mid-August (Sedivec et al., 2009).

Sampling Scheme

In order to investigate the relationship between plant performance and seed source in prairie restoration, *A. gerardii*, *S. nutans*, and *B. curtipendula* seeds were hand collected from remnant and restored prairies in Solem and Urness Townships, located in Douglas County in rural western Minnesota, USA (centered near 45°49' N, 95°43' W). In addition, seeds of all three species were purchased from three Minnesota nurseries that specialize in wild seed production for conservation purposes.

In August 2009, remnant and restoration seed sources were identified for the presence and relative abundance of the three study species. Sites were defined as remnants if there was no history of plowing and were typically found on hillsides too steep for agricultural production, in fence corners inaccessible to farm machinery, along roadsides. Locations with a history of row-crop production that were subsequently replanted with native seeds following Minnesota

guidelines were designated as restorations. Permits were acquired for a total of fifteen remnant and ten restoration sites (Figure 1).

Seeds were hand collected on cool, clear days between August 31st and September 26th from approximately 50 randomly selected individuals of each species at each location. All seeds from each individual were placed in labeled manila coin envelopes, one envelope for each maternal line. The identity of each maternal line was maintained throughout the study. I used two strategies to randomize sample collections. For larger sites, I assessed the shape and size of the restoration, and selected random transect starting points along one side of the perimeter. I then harvested seeds at regular intervals along each transect, bisecting the site. For smaller sites, I used a random number list to count out a random selection of 50 maternal plants. In some cases, sites had smaller populations, and fewer maternal lines were sampled from these locations. A total of 2,891 individual plants were sampled, 943 of *A. gerardii*, 978 of *S. nutans*, and 970 of *B. curtipendula*.

Coin envelopes from each collection were placed in plastic freezer bags with 5 gram silica gel desiccant packs (ULINE), and transported to the Chicago Botanic Garden (Glencoe, IL) where they were transferred to paper grocery bags and stored in a seed dryer at 14°C and 15% relative humidity.

A randomized subset of *A. gerardii* and *S. nutans* envelopes from each source population were selected to be cleaned, counted and weighed. Coin envelopes were emptied into 16 grade lab test sieves and a rubber stopper was used to gently break the spikelets and allow the seeds to pop out and fall through the mesh into a collecting pan. The chaff was then broken up and sifted through a 20-grade lab test sieve, and residual seeds were collected. To collect any remaining

seeds, the chaff was then poured out onto white paper and a table magnifier used to verify that all seeds had been cleaned and counted. Cleaned seeds from each maternal line were weighed. Due to its unique morphology, *B. curtipendula* samples were not cleaned, however the spikelets from each maternal line used in the study were counted and weighed.

The seed count data for *S. nutans* was used to determine which source populations to use in the field experiments. Three restoration source populations were chosen, one state, one federal, and one private (Hegg Lake Hill, Runestone WPA, and Mahoney's restoration). Due to a lower seed set in remnant populations, four remnant sources were selected (Staffanson Prairie, JI Case Hill, Hegg Lake NE Corner, and Hegg Lake East Unit). Seeds were also purchased from three Minnesota native seed nurseries (Prairie Restorations Inc., Habitat Forever LLC, and Prairie Moon Nursery Inc., Table 1).

Provenances

Staffanson Prairie (45°81'05"N 95°75'04"W, 45-ha), is a virgin prairie preserve owned and managed by The Nature Conservancy (TNC). The land was acquired in 1972 from the Staffanson family, who had owned the land since 1930. The southern and eastern edges of the property had been cultivated with flax and grains, and the prairie was hayed annually until 1980. Since acquisition, TNC has conducted prescribed burns every four years to maintain the prairie and a variety of management techniques have been used to control invasive non-native plants threatening the diversity of the prairie. Seeds for this study were collected from the east unit of the preserve (approximately 17-ha), which had been burned in spring 2009 (The Nature Conservancy, 2011).

JI Case Hill (45°85'98"N 95°64'19"W, 2.3-ha), is a roadside prairie remnant situated on a steep hill which is a challenge to climb on foot, much less with a tractor. Located at the corner of County Road 15 and Tower Hill Road SW, cater-corner from the JI Case WPA, the remnant is unmanaged except for annual mowing of the strip of prairie immediately next to the road. Due to the patch distribution and comparatively small populations at this site, I used the second, small site strategy for seed collection at JI Case Hill.

Hegg Lake WMA (45°76'N 95°67'W), is 140-ha unit, approximately 42-ha of which is now tallgrass prairie, some remnant and some restored (Minnesota Department of Natural Resources, 2011). Wildlife management areas (WMAs) are part of Minnesota's outdoor recreation system and are established to protect those lands and waters that have a high potential for wildlife production, public hunting, trapping, fishing, and other compatible recreational uses. This system started in 1951, when Minnesota's Department of Natural Resources (DNR) established its "Save the Wetlands" program to buy wetlands and other habitats from willing sellers to address the alarming loss of wildlife habitat in the state.

The Hegg Lake WMA was established as part of this effort. The land was purchased in two parcels, a larger unit from Mr. Mel Hagen in 1961, and a smaller unit from Mrs. Viola Brown in 1962. Approximately 53-ha of the site is designated as wetland, the majority of which had been drained for agricultural use prior to the state's purchase of the land. During the '60s and '70s, the wetlands were restored and set aside as a wildlife preserve, but most of the remaining land stayed in production. The DNR began restoring the rest of the lots during the mid-90s. Tallgrass prairie areas were planted using native seed sourced from remnants in Fergus Falls in Otter Tail County, MN (approximately 80 km NW of the study area) and from the Bill Freeman WMA located in

Stevens County, MN (approximately 43 km SW of the study area). Since the prairie restoration was established, the DNR has conducted prescribed burns every 4-5 years and used a variety of management techniques, including periodic spraying, mowing, and haying, to control invasive and exotic species.

For this study, remnant seeds were collected from two areas on the site: Hegg Lake NE Corner (45°76'69"N 95°65'87"W, 2.5-ha) and Hegg Lake East Unit (45°76'81"N 95°67'38"W, 5.7-ha). Restoration seeds were collected from a tract planted in 1999, Hegg Lake Hill (45°76'64"N 95°67'65"W, 2.4-ha).

Runestone WPA (45°80'31"N 95°65'60"W, 8.2-ha), is a federal waterfowl production area (WPA) managed by the USFWS Fergus Falls Wetland Management District. Prior to its purchase in 1988, the land was largely in row-crop production, with some remnant wetland areas (approximately 0.15-ha). The site was planted with corn in 1989, and soy in 1990 and 1991. Native warm-season grasses were seeded after harvest in 1991 with seeds sourced from production plots located in Fergus Falls in Otter Tail County, MN (approximately 80 km NW of the study area). These production plots were established using seeds from a number of prairie remnants located in Otter Tail County. The restoration was subsequently augmented with purchased cool-season grasses, but no forb species have been planted. The site is burned every 5-7 years, and is periodically mowed or sprayed to control invasive and exotic species.

Mahoney's Restoration (45°79'94"N 95°68'34"W, 6-ha), is a private restoration owned by Robert D. Mahoney as part of the USDA Conservation Reserve Program (CRP). Through this program, agricultural landowners can receive annual rental payments and cost-share assistance to establish long-term, resource-conserving covers on eligible farmland (Farm Service Agency,

2011). Over time, CRP restoration guidelines have been updated to incorporate current best practices. In 2005, Mahoney planted a 2-ha unit was planted with a native seed mix sourced from Heartland Conservation Services (Alexandria, MN). It is burned approximately every five years and mowed as necessary to control thistles and other weedy exotics.

In March 2010, *A. gerardii*, *S. nutans*, and *B. curtipendula* seeds were purchased from three Minnesota nurseries, Prairie Restorations, Inc., Habitat Forever, LLC, and Prairie Moon Nursery, Inc., which specialize in wild seed production for conservation purposes. **Prairie Restorations, Inc.** plant materials were sourced from prairie remnants located Sherburne County, MN (approximately 160 km SE of the study area). Seeds were produced in bulk lots at the Bluestem Farm, located on the eastern edge of the Red River Valley near Moorhead, MN (approximately 160 km SE of the study area). **Habitat Forever, LLC** obtains seeds from Feder's Prairie Seed Company, which has seed production lots in Blue Earth, Faribault County, MN (approximately 320 km SE of the study area). Each species purchased from Feder's had a different genetic source. *A. gerardii* seed was collected from remnants in Polk County, MN (approximately 250 km NW of the study area), *S. nutans* from remnants in Kittson County, MN (approximately 370 km NW of the study area), and *B. curtipendula* from remnants in Houston County, MN (approximately 470 km SE of the study area). Similarly, plant materials from **Prairie Moon Nursery, Inc.** came from a variety of genetic origins. The *A. gerardii* was gathered from remnants in Dunn County, WI (approximately 340 km SE of the study area), *S. nutans* from remnants in Green County, WI (approximately 528 km SE of the study area), and *B. curtipendula* was assembled from remnants in Houston County, MN (approximately 470 km SE of the study area) and from Crawford County, WI (approximately 550 km SE of the study area). Seeds were

produced in bulk lots located in Houston County, MN (approximately 470 km SE of the study area). All nursery seeds arrived at the Chicago Botanic Garden uncleaned, and were stored in their original packaging in the seed dryer with the rest of the source material until they were needed (Figure 2).

Experimental Design

Three plots were established in three existing restorations in the study area to test for differences in establishment and growth of three species, grown from four local remnants, three local restorations, and three Minnesota nursery seed sources. Nested within each remnant and restoration site were the individual maternal lines. For each species, an equal number of seeds from each remnant and restoration maternal line, as well as thirty samples, each containing twenty randomly selected seeds from each nursery source, were randomly selected and sown into three common garden plots. Plots were planted at each of the restoration source locations: Hegg Lake Hill, Runestone WPA, and Mahoney's restoration.

In order to investigate what influence, if any, use of plugs versus seed has on seedling survival and establishment in restorations, up to nine seeds from each maternal line, along with thirty samples (nine seeds/sample) from each nursery source, were germinated and grown into plugs in a controlled growth chamber environment prior to planting them in the same three common garden plots. The realized experimental design was unbalanced due to unevenness in the quantities of seeds produced by the maternal lines.

Common garden studies, where seeds from multiple maternal plants of a species are sampled from one or more identified geographic areas and planted in a common environment using a randomization scheme, provide a powerful tool for determining whether observed phenotypic

differences among populations are genetically based (Hufford & Mazer, 2003; Kramer & Havens, 2009). In the common garden plots environmentally induced phenotypic differences between the plants are minimized, allowing observation and comparison of genetically based traits. By looking at seed germination and plant performance in a controlled environment and again in three common garden plots, I will be able to quantify source population differentiation in plant performance.

Growth Chamber Experiment

Germination in growth chambers

Between May 3rd and June 6th 2010, a subset of seeds (or spikelets in the case of *B. curtipendula* and nursery materials) from each of the selected remnant, restoration, and nursery sources were germinated under controlled conditions in growth chambers at the Chicago Botanic Garden. For each of 734 maternal lines (238 *A. gerardii*, 286 *S. nutans*, and 210 *B. curtipendula*), seeds were randomly sampled and placed in 60-mm-diameter Petri dishes lined with labeled blue seed germination blotters (Anchor Paper Company, St. Paul, MN). For maternal lines with fewer than 18 seeds, half were chosen at random for the germination study (for odd numbers, the lesser quantity was used). Maternal lines that produced fewer than two seeds were excluded from the study. An equal number of spikelets, 279 of each species, were randomly selected from each nursery source. There were 2300, 2223, and 2511 seeds from remnant, restoration, and nursery source types respectively. Of those, 1778 were *A. gerardii*, 2585 were *S. nutans*, and 2671 were *B. curtipendula* (n = 7034).

Planting sprouts into plug trays

Dishes were kept moist with distilled water and placed on trays. Dish trays were rotated and watered every 48 hours and kept in a growth chamber on a 18.3/21.1°C night/day rotation and a

"natural" light schedule, starting with 14h20min of fluorescent light and increasing 2min40sec each day. Germination was assessed daily and seeds were removed when the radicle emerged at least 1 mm. Each seed with an emerged radicle (sprout) was placed in a randomly determined plug in one of nine 12 × 24 plug trays. Plugs were 2 cm square on top and tapering below, 4.5 cm deep, and filled with Sunshine plug mix (Sun Gro Horticulture, Vancouver, BC). Two sets of nine plug trays, for a total of 18, were used. Sprouts were not placed in edge plugs, nor were sprouts from the same dish ever placed in duplicated trays (i.e. Trays 9.1 and 9.2 would not have sprouts from the same dish). Plug trays were rotated and watered from below three times a week and kept in the same growth chamber as the dishes. The 7034 seeds placed in petri dishes yielded a total of 3040 sprouts, 680 remnant, 1191 restoration, and 1169 nursery, representing 599 maternal lines.

Common Garden Experiment

Preparation of seeds for direct planting

All remaining seeds from each maternal line were set aside to be planted directly into the common gardens. A total of 2219 *A. gerardii* (689 remnant and 1530 restoration), 8296 *S. nutans* (4486 remnant and 3810 restoration), and 3623 *B. curtipendula* (2087 remnant and 1536 restoration) seeds were divided using randomized selection into three groups and placed in new labeled coin envelopes. In addition, for each species, thirty labeled coin envelopes from each nursery source were filled with twenty randomly selected spikelets and randomly divided among the three groups (1800 spikelets per species). Each group was sorted into cardboard boxes, sealed into plastic freezer bags with 5 gram silica gel desiccant packs. A total of 19547 seeds were set aside to be planted directly in the three common garden plots.

Transportation & Site Preparation

On May 19th, 2010 the 18 plug trays and the plastic bags containing the three groups of sorted seed envelopes were transported in an air-conditioned car to Kensington, MN. Each plug tray was covered with a clear plastic lid and sealed with duct tape. Plants were allowed to acclimate to Minnesota conditions for three weeks prior to planting. Plug trays were rotated and watered daily. Sprout survival and growth (number and length of leaves) was recorded prior to transplantation into the common garden plots. Of the 3040 sprouts, 1070 survived to be planted, 127 remnant, 370 restoration, and 573 nursery.

Planting Common Garden Sites

Between July 7th and 9th, 1070 plug-seedlings and 19547 seeds were randomly planted into three 10 x 10 meter experimental common garden plots located at each of the restoration source sites (Hegg Lake Hill, Runestone WPA, and Mahoney's restoration). Each plot was prepared by mowing, and ten rows measured out and marked with flags. Sprouts were planted at 1/8 meter spacing within rows, and 10 cm and 1m alternating spacing between rows. A toothpick was placed to 1 cm to the east of each sprout. Seeds were planted at the same intervals as the sprouts. For locations with sprouts, seeds were planted 1cm east of the sprout's toothpick. Seeds were carefully poured from each coin envelope in a line along the row, firmly pressed into the soil, and toothpicks were placed on either side of the line of seeds. Each row was watered immediately after planting.

Field-seedling measurements one month after planting

Seedlings grown in plug trays will hereafter be referred to as "plug-seedlings" and seedlings from seeds sown directly in the field will be referred to as "field-seedlings." Field-seedling germination and growth was assessed between August 7th and 10th, 31-34 days after planting

(hereafter one month). Measurers recorded the number of seedlings and the height of the longest leaf for each seedling at each position. Positions were skipped when the toothpicks had fallen over or were missing because the seedlings could not be positively identified.

Field and plug-seedling measurements two months after planting

Beginning in August, a randomly selected row was monitored weekly for sprout and seedling survival and growth in order to assess when plants began senescing. Field-seedlings began to senesce in the last week of August, and plug-seedlings in the second week of September. Final field-seedling measurements, including germination, survival, and growth (height of the longest leaf for each field-seedling) were taken between August 28th and September 6th, 52-61 days after planting (hereafter two months). Final plug-seedling measurements, including survival and growth (number of leaves and height of the longest leaf for each plug-seedling) were recorded between September 11th and 13th, 66-68 days after planting (hereafter two months).

Data collection for the entire study was “blind” in the sense that the measurer identified the seed, seedling, or plant by a randomly assigned number or row/position combination.

Statistical Analysis

Each species were analyzed separately. Plug- and field-seedlings were excluded from analyses when their identity was ambiguous or unknown, either due to lost toothpicks or otherwise. *A. gerardii* seeds from JI Case Hill were excluded from plug-seedling analyses because only one sprout germinated. *A. gerardii* seeds from both JI Case Hill and Runestone sources were excluded from field-seedling analyses due to an almost a complete absence of germination (Runestone had two seedlings, JI Case Hill had none). All statistical analyses were performed using the statistical package R (R Development Core Team, 2010).

Field-Seedlings:

Performance in field-seedlings was assessed separately one and two months after planting. Field-seedlings that germinated during the first month were included in the germination analysis. The survival analysis included all field seedlings that germinated during the first month and those that sprouted after the first assessment.

I used a binomial family generalized linear model (GLM) to assess field-seedling emergence and field-seedling survival. The residual deviance of the full model greatly exceeded the residual degrees of freedom, indicating over-dispersion; therefore I used the quasibinomial family for analysis.

To analyze field-seedling vigor, one and two months after planting done separately, I used log-transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection.

For all analyses, I used backwards elimination of non-significant variables (at $p = 0.05$) to select the minimal adequate models (Crawley, 2005). My initial explanatory variables included common garden site (Hegg Lake Hill, Runestone WPA, Mahoney's restoration), seed source type (remnant, restoration, nursery), and seed source nested within seed source type (10 seed sources). In cases where source type and source nested within source type were not significant, I conducted a second round of model selection with site and source as the only explanatory variables. As an alternative approach, I used step-wise *a posteriori* deletion of the 10 seed sources to examine how sources grouped within types (Crawley, 2005).

Sprouts & Plug-Seedlings:

I used a binomial family generalized linear models (GLM) to assess germination and survival of plants in the growth chamber experiment separately at four stages: sprout, when the radicle emerged at least 1 mm and sprouts were planted in the plug trays; plug, when sprouts grew at least one leaf in the plug trays; planting, when plug-seedlings were planted in the field plots; two months, when plug-seedlings had been in the field plot for two months. The residual deviance of the full model did not exceed the residual degrees of freedom, therefore, I report results from the GLM using the binomial analyses.

Plug-seedling vigor was analyzed separately at two stages: plug and two months. At the plug stage (prior to planting), I used leaf count as the response for general linear model selection with poisson errors. I did not analyze leaf length at the plug stage because plug measurements took place over the course of a month. For analyzing plant vigor two months after planting outside, I used height of the longest leaf as the response for linear model selection and total leaf count as the response for general linear model selection with poisson errors.

For all analyses, I used backwards elimination ($p = 0.05$) to select the minimal adequate models. At the sprout, plug, and planting stage, my initial explanatory variables included seed source type (remnant, restoration, nursery), seed source nested within seed source type (10 seed sources). For analyses with responses at the plug and planting stages I also included tray as a factor. At the final stage I included common garden site (Hegg Lake Hill, Runestone WPA, Mahoney's restoration), seed source type (remnant, restoration, nursery), and seed source nested within seed source type (10 seed sources). In cases where source type and source nested within

source type were not significant, I conducted a second round of model selection with site and source as the only explanatory variables.

RESULTS

Growth chamber experiment

Germination

Germination of seeds in the growth chambers differed significantly among seed sources for all species ($p < 0.0001$ for all species, Figure 5). In addition, germination differed significantly among sources of the same type (i.e. remnant, restoration, and nursery seed sources, $p < 0.0001$ for all species, Figure 5). However, specific sources and source types did not perform consistently among species (Figure 5, Table 2).

Andropogon gerardii seeds from two of the nursery sources (Prairie Moon and Habitat Forever) and one restoration (Hegg Lake Hill) had the highest mean germination rates ($73.9 \pm 1.8\%$, $74.9 \pm 1.0\%$, and $88.2 \pm 1.1\%$ respectively); nearly twice that of the other restorations and remnant sources and more than five times higher than the third nursery source (Prairie Restorations Inc, $13.9 \pm 1.8\%$, Figure 5). *Bouteloua curtipendula* seed germination rates for all of the nursery and restoration sources exceeded those of remnant sources by at least 25%, with one nursery (Habitat Forever) and two restoration sources (Hegg Lake Hill and B. Mahoney) exceeding them by more than 50% (Figure 5). In contrast, mean germination of *Sorghastrum nutans* nursery sources was 30-39% lower than seeds from restoration sources and 14-27% lower than remnant sources (Figure 5).

Survival

Plug-seedling survival at the plug and planting stages differed significantly among seed sources and source types for all species, although performance differed among species ($p < 0.0001$ for all species at both stages, Figure 5). Between germination and planting, mean survival among all *A. gerardii* plug-seedlings was 32%. *A. gerardii* nursery survival (64.3 ± 3.1 %) was three times greater than that of restoration plug-seedlings (20.4 ± 2.3 %) and more than five times greater than remnant plug-seedling survival (11.8 ± 3.4 %, Figure 5). *B. curtipendula* plug-seedlings survival pre-planting was highest among the three species (58%) and generally high among all seed sources (52-78%), with the exception of one nursery source (Habitat Forever) which had the lowest survival rate (38.2 ± 1.1 %). Twenty-one percent of *S. nutans* plug-seedlings survived to planting, however survival among *S. nutans* nursery sources (except Prairie Restorations Inc.) was two times greater than restoration and four times greater than remnant sources at the plug and planting stages.

Common Garden Experiment

Field-seedling Germination & Survival

The influence of seed source and common garden site on germination of seeds sown directly in the field and field-seedling survival until two months after planting varied among species. *A. gerardii* and *B. curtipendula* seed germination and field-seedling survival differed significantly among seed sources and among common garden sites ($p < 0.0001$ for both species, Figure 3, Figure 4, Table 2). Mean germination of Prairie Moon and Habitat Forever *A. gerardii* seeds in the field (11.4 ± 3.2 %) were double that of remnant seeds (5.2 ± 3.7 %, Figure 3). Mean field germination of *B. curtipendula* seeds from nursery sources (21.1 ± 2.7 %) and restoration sources (21 ± 3 %) were more than two times greater than remnant sources (9 ± 2 %, Figure 3). Mean

germination and survival of *A. gerardii* and *B. curtipendula* field-seedlings was more than two times higher at the B. Mahoney common garden site and than at Runestone; although three sources performed best at Hegg Lake Hill (*A. gerardii* from Hegg Lake East Unit, and *B. curtipendula* from Prairie Moon and B. Mahoney), and all of the *A. gerardii* remnant field-seedlings performed worst at Hegg Lake Hill (Figure 3).

In contrast, the impact of source on germination of *S. nutans* seeds sown directly in the field varied among common garden sites, as evidenced by a significant interaction term ($p = 0.013$, Figure 3). *S. nutans* survival until two months after planting differed significantly among common garden sites ($p < 0.0001$) but seed source was not a significant factor ($p = 0.74$, Figure 4). Mean germination and survival of *S. nutans* restoration and remnant field-seedlings was between 1.5 and 4.5 % higher at the B. Mahoney common garden site and than at the other two sites (Figure, 3, Figure 4). However, nursery seeds had the highest mean germination of all source types ($3.5 \pm 1.2\%$) at Hegg Lake Hill common garden site, but the lowest germination at the other sites (Runestone: $0.5 \pm 0.4\%$, B. Mahoney: $2.3 \pm 1.1\%$, Figure 3).

In all species, field-seedlings from the third nursery source (Prairie Restorations Inc.) experienced significantly lower germination and survival than the other two nursery sources ($p < 0.05$); *S. nutans* Prairie Restorations Inc. field-seedling germination was less than 2% at all common garden sites (Figure 3).

Plug-seedling Survival

Plug-seedling survival two months after planting in the common garden sites was low for all species (87-90%), differed significantly among seed sources ($p < 0.0001$ for all species), but was not influenced by common garden site ($p > 0.1$ for all species, Figure 5, Table 2).

Field-seedling Vigor

For all species, field-seedling vigor (aggregate longest leaf height) was significantly different among seed sources both one and two months after planting ($p < 0.05$ all species at both time periods, Figure 6, Figure 7, Table 2). Plant vigor differed significantly among common garden sites one (Figure 6) and two months (Figure 7) after planting for *S. nutans* (one month $p = 0.002$, two months $p = 0.013$) and *B. curtipendula* field-seedlings (one month $p = 0.027$, two months $p = 0.001$), but did not influence *A. gerardii* field-seedling vigor (one month $p = 0.102$, two months $p = 0.102$). As with field-seedling germination and survival, field-seedlings from nursery sources generally had higher plant vigor than remnant and restoration sources, *A. gerardii* nursery field-seedlings were more than double the size of remnant seedlings (Figure 6, Figure 7). Performance among remnant and restoration sources was more varied within source types and among species (Figure 6, Figure 7).

The effect of seed source type on *B. curtipendula* field-seedling vigor varied among common garden sites as evidenced by a significant interaction term (one month $p = 0.035$; two months $p = 0.009$, Figure 6, Figure 7). Plant vigor of *B. curtipendula* field-seedlings from two nurseries (Prairie Moon and Habitat Forever) was more than two times greater than the third nursery source (Prairie Restorations Inc.) at all common garden sites both one and two months after planting (Figure 6, Figure 7). Even so, mean seedling vigor of all nursery sources was 1.2-2.5 times greater than that of the restoration sources (across common garden sites) and between 1.8-4.7 times greater than mean seedling vigor of all remnant sources (across common garden sites, Figure 6).

Plug-seedling Vigor

Plug-seedling vigor (longest leaf) two months after planting differed significantly among common garden sites for all species ($p < 0.0001$ for all species, Figure 8, Table 2), while source had a significant influence on leaf length for *S. nutans* ($p < 0.0001$) and *B. curtispindula* ($p < 0.0001$), but not for *A. gerardii* ($p = 0.393$, Table 2). All plug-seedlings, regardless of source or species, were tallest at the B. Mahoney site and most were shortest at Runestone (Figure 7). In fact *B. curtispindula* plug-seedlings at B. Mahoney's restoration were an average of 8 cm (± 2 cm) taller than those at Hegg Lake Hill and 12 cm (± 2 cm) taller than Runestone plug-seedlings. The sole exception were *S. nutans* plug-seedlings grown from JI Case Hill seeds, which were an average of 4 cm (± 5 cm) taller at Hegg Lake Hill than at B. Mahoney's site and a full 10 cm (± 5 cm) taller than plug-seedlings at Runestone.

The effect of seed source and common garden site on plug-seedling leaf count two months after field planting, however, differed among species. *B. curtispindula* plug-seedlings were significantly influenced by both site and source, and sources grouped by source type ($p < 0.001$, Figure 8). Interestingly, *B. curtispindula* plug-seedlings from restoration seed sources had 2-4 more leaves than other sources at the B. Mahoney and Hegg Lake Hill common garden sites. Also, *B. curtispindula* restoration and nursery plug-seedlings had higher leaf counts at Hegg Lake Hill common garden site and lower counts at Runestone (Figure 8). Leaf count of *S. nutans* plug-seedlings also differed significantly among common garden sites ($p = 0.0001$), but not by source ($p = 0.38$, Figure 8). Neither common garden site ($p = 0.1$) nor seed source ($p = 0.95$) had a significant impact on leaf count for *A. gerardii* plug-seedlings two months after planting (Figure 8).

Plant Performance: Seeding Method

The influence of seed source and common garden site on seedling performance, in terms of germination, survival, and vigor, differed between plug-seedlings and field-seedlings and varied among species. For some species the effect of seed source was dependent on common garden site, but this too differed between plug and field-seedlings of the same species. For example, common garden site and seed source had an interactive effect on *S. nutans* field-seedling germination ($p = 0.013$), but common garden site alone influenced survival ($p < 0.0001$), and both were important to *S. nutans* seedling leaf length ($p < 0.01$ field and plug).

In addition, planting method had a strong influence on overall plant establishment. Germination of seeds sown directly into the common garden sites was quite low, with *B. curtipendula* having the highest germination (17%) and *S. nutans* the lowest (3%, Figure 3). Field-seedling mortality was also low ($< 1\%$ for all species, Figure 4). In fact, between one and two months after planting, the number of field-seedlings that died for each species was lower than the number of new sprouts. In contrast, germination of seeds in the growth chambers was 3-12 times higher than field-seedlings, *B. curtipendula* the highest (50%) and *S. nutans* the lowest (36%, Figure 5). Plug-seedling mortality over the course of the experiment was much higher than for field-seedlings for these plants (50-82%, Figure 5). Nevertheless, despite the higher rate of mortality, survival was 3-6 times higher for plug-seedlings than for field-seedlings (Figure 3, Figure 5).

DISCUSSION

Does seed source of dominant grasses influences germination and performance during prairie restoration establishment?

Seed source had a significant impact on *Andropogon gerardii*, *Sorghastrum nutans*, and *Bouteloua curtipendula* seed germination and seedling performance during early establishment. In addition, when seed source was significant, plant performance was usually similar among sources of the same type (i.e. remnant, restoration, and nursery seed sources). However, specific sources and source types did not perform consistently among species or even between planting methods.

In controlled and field restoration conditions *A. gerardii* and *B. curtipendula* from remnant sources had lower germination rates and seedlings were less vigorous than those from restoration and nursery seed sources. Mean germination rates of *B. curtipendula* (field: $26 \pm 3\%$, GC: $69.77 \pm 1.11\%$) and *A. gerardii* (field: $11.4 \pm 3.2\%$, GC: $42.68 \pm 3.37\%$) seeds from two of the nursery sources (Prairie Moon and Habitat Forever) were two times higher than remnant sources, both in the field (*B. curtipendula*: $9.02 \pm 2.08\%$, *A. gerardii*: $5.22 \pm 3.73\%$) and in the growth chambers (*B. curtipendula*: $21.1 \pm 2.0\%$; *A. gerardii*: $42.68 \pm 3.37\%$).

Moreover, *A. gerardii* nursery field-seedlings were more than double the size of remnant seedlings and *B. curtipendula* field-seedlings from two nurseries (Prairie Moon and Habitat Forever) were twice as vigorous as restoration seedlings and 2-5 times more vigorous than remnant seedlings both one and two months after planting. *Sorghastrum nutans* remnant and nursery field-seedlings did not group by source type and none of the sources performed consistently better. These results demonstrate that seed source, both under idealized conditions (i.e. growth chamber experiment) and under restoration conditions (i.e. common garden

experiment), has an important impact on seed germination and seedling performance during restoration establishment.

The higher germination rates and greater vigor of most of the nursery and restoration seed sources, especially among *A. gerardii* and *B. curtipendula* seedlings, are inconsistent with the expectation that seeds sourced from local remnant populations would perform better than those of non-local provenances (Wilkinson, 2001; McKay et al., 2005). Moreover, these results seem to indicate that using seeds originating from "as close to the restoration site as possible" as mandated by the 2009 Minnesota legislation may result in restoration projects with grasses that suffer from low germination and poor establishment (Minnesota Department of Natural Resources, 2009). However, there are several considerations that practitioners should take into account prior to making any decisions.

Restoration versus remnant environmental conditions

The higher seed germination and establishment vigor of *A. gerardii* and *B. curtipendula* field and plug-seedlings from nursery and restoration sources in the common garden sites may be unsurprising in light of the very different competitive and environmental selection pressures plants in production lots and restorations are under compared to those in remnant populations.

The competitive ability of the dominant prairie grasses is a key factor in community functioning (Weaver & Fitzpatrick, 1932; Weaver, 1954). The community dynamics in most remnant prairies have been severely altered over time. Due to habitat fragmentation and other changes in land-use, remnants today likely lack the full complement of natural processes, including large migratory herbivores, historic fire regimes, and disrupted gene flow among populations (Jackson, 1999; Gustafson et al., 2004a; Wilsey, 2010; Yurkonis et al., 2010b). Even

so, inter- and intra-specific competition in prairie fragments almost certainly exerts enormous selective pressure on plant populations. Seedlings compete with other plants and dead plant-material for light and with a dense network of roots for nutrients and water (Weaver & Fitzpatrick, 1932; Weaver, 1954). The competitive environment for seedling recruitment in prairie remnants is intense and likely quite different from the conditions during restoration establishment.

Most restoration sites, including the three used in this study, were previously in agricultural production, subject to long-term tillage and herbicide use, which likely altered the many ecosystem processes of the site in important ways (Silletti & Knapp, 2001; Wilsey, 2010; Klopf & Baer, 2011). During restoration, land managers will take steps to reduce plant competition and enhance seed-soil contact prior to planting (Schramm, 1990). They will mow, use herbicides, or plant native seeds into harvest stubble left over from the season prior (Schramm, 1990; Hier et al., 1999). Given the potential land-use legacy due to long-term agricultural use and the high light, low-competition environment, it is likely that seeds from prairie remnants are not suited to conditions of restoration establishment. Moreover, under the conditions of seed production fields, it is entirely possible that significant shifts in genotypic frequency may have occurred in a relatively short period of time that resulted in seeds from nursery and restoration sources becoming adapted to restoration establishment conditions. In this study, seeds and plug-seedlings were sown into three already existing restorations, and so this experiment did not reproduce restoration establishment conditions exactly. Nevertheless, even in this high light, high-competition environment germination of *A. gerardii* and *B. curtipendula* field-seedlings from nursery and restoration sources was more than twice that of remnant sources. This suggests the

possibility that, at least during the first growing season, seeds from nursery and restoration sources are better adapted to restoration conditions than seeds from remnants.

Remnant sources may be better adapted in the long-term

Other studies have found evidence that plants grown from local sources do not always perform better than those from non-local sources when it comes to seed germination and early seedling establishment (Bischoff et al., 2010; Seifert & Fischer, 2010; Miller et al., 2011). It is possible that remnant populations may be maladapted to the restoration sites. Not all populations are optimally adapted to their environment (Lesica & Allendorf, 1999; Sackville Hamilton, 2001). In fact, it is possible to find other, non-local populations which may have equal or even greater fitness than the local ecotypes, especially for more long-lived species (Lesica & Allendorf, 1999; Sackville Hamilton, 2001). Environmental changes may have resulted in disruptions of local adaptations or the remnant source populations may be unsuitable because of restoration practices (Bischoff et al., 2010).

This study covered germination and survival during the first growth season, generally considered to be crucial phases for restoration establishment (Seifert & Fischer, 2010). However, other important metrics of adaptation exist which may impact the long-term success of restorations. While plants from local sources may not always have higher germination or greater plant vigor, some studies have found such plants may possess other adaptive traits that may have more of a long-term impact on restoration success. For example, while multiple native species have been shown to inhibit exotic establishment, several studies have found that this ability to hinder invasion decreased with the distance between the source population and the experimental site (Seabloom et al., 2003; Gustafson et al., 2005; Bischoff et al., 2010; Middleton et al., 2010;

Yurkonis et al., 2010a; Yurkonis et al., 2010b; Stevens & Fehmi, 2011). In a study comparing restorations with local and non-local provenances, *A. gerardii* plants from non-local sources had higher insect damage, were less vigorous, and were phenologically behind the local-source plants (Gustafson et al., 2001). In addition, significant differences in root morphology between cultivar and non-cultivar *A. gerardii* (Klopf & Baer, 2011). Given the geographical and environmental variation in Minnesota, comprising four hardiness zones and three biomes, and given that the seeds used in this study were from sources from across the state, it may be that important variation in growth form, phenology, or competitive ability exists that was not captured in this investigation (Moncada et al., 2007; Wilsey, 2010).

Variation among remnants may be the result of genetic drift or parental effects

Population differentiation in plants is the result of various evolutionary processes, including differential responses to geographically-localized selection pressure, genetic drift, and inbreeding (Hufford & Mazer, 2003; Kramer & Havens, 2009). If differential selection pressure is strong enough, populations will accumulate adaptive traits and become genetically distinct from each other (Bischoff et al., 2010). Multiple studies have found evidence of both genetic and adaptive morphological differentiation in dominant prairie grass species across a larger, interstate geographic scale (Gustafson et al., 2001; Schultz et al., 2001; Gustafson et al., 2002; Gustafson et al., 2004a; Gustafson et al., 2004b; Gustafson et al., 2005). Schultz *et al.* (2001) found that *A. gerardii* plants from Kansas had significantly courser root systems and invested more in symbiotic associations with mycorrhizal fungi (AMF) than did plants from Illinois. In common garden studies and competition experiments *A. gerardii* plants from Kansas were half the size of local Illinois and cultivar plants (Gustafson et al., 2002; Gustafson et al., 2004b).

At a more local intrastate scale, multiple studies have found evidence of population-level genetic differentiation among prairie remnants in multiple grass and forb species (Gustafson et al., 2001; Gustafson et al., 2002; Gustafson et al., 2004a; Gustafson et al., 2005; Dolan et al., 2008). However, the while genetic relationships of some of these native species have varied with geography, others have not. Gustafson *et al.* (2002; 2005) found that the genetic relationships among *Dalea purpurea* (purple prairie clover) populations in Illinois correlated well with geographic proximity. In contrast, genetic analyses of three prairie species from multiple Minnesota remnants found significant population level genetic differentiation, but the patterns of variation did not relate to distance or to ecoregion (Moncada et al., 2007). The presence of strong genetic differentiation among local populations indicates that contemporary gene flow among prairie remnants is limited, perhaps due to intense habitat fragmentation.

Given that habitat fragmentation is ubiquitous in the North American prairie ecosystem, small remnant populations may be genetically depauperate, due to reduced gene flow, inbreeding or genetic drift (Hufford & Mazer, 2003; Gustafson et al., 2004a; Ouborg et al., 2006; Kramer & Havens, 2009). Studies of dominant grass species (including *A. gerardii* and *S. nutans*) have found no association between genetic diversity and the size of the remnant (Gustafson et al., 2001; Gustafson et al., 2002; Gustafson et al., 2004a; Gustafson et al., 2004b; Gustafson et al., 2005; Moncada et al., 2007; Dolan et al., 2008). Suggesting that even extremely small remnant populations may possess a substantial amount of genetic variation. Interestingly, seeds from less-connected populations have been shown to have lower establishment in new sites than seeds of more-connected ones (Seifert & Fischer, 2010). Moreover, seeds from smaller sites had greater variability in germination and plant vigor when planted in new sites than seeds from larger

populations (Seifert & Fischer, 2010). These results combined with the patterns of germination and plant performance found in this study, suggest that fine-scale population differentiation in grass species may be strongly influenced by genetic drift or fine-scale environmental variation.

Common garden studies cannot detect whether morphological differences are due to genetic drift, adaptation, or maternal effects (Hufford & Mazer, 2003; Pujol et al., 2008; Kramer & Havens, 2009). It is possible that at a fine-scale, genetic drift is stronger than differential selection. To detect whether variation among remnant populations is the result of genetic drift, common garden studies or reciprocal transplant experiments should be combined with genetic analyses (Hufford & Mazer, 2003; Moncada et al., 2007; Kramer & Havens, 2009). Even though all the remnant sources in this study were within an 8 kilometers of each other, it is also conceivable that differences in parental environment (e.g. competition, sunlight, plant diversity, fire-regime, etc.) may explain some of the variation in remnant seedling performance (Galloway, 2001; Pujol et al., 2008). To determine the extent to which parental environment influences seed performance in restorations, it would be necessary to plant seeds of known pedigree into multiple restoration sites and test for variation in offspring performance. In either case, using seed from multiple local remnants may result in the creation of restorations that may have the reassembled genetic history of an un-fragmented prairie

Protecting existing native prairies from genetic contamination

The seeds purchased from nurseries and the source seed used to plant the restoration sites used in this study were initially grown in production fields using multiple remnant sources. However, the nursery sources in this study had origins between 160 and 550 kilometers away from the common garden sites. Seedlings from these sources were typically more vigorous than

other sources. *Andropogon gerardii* nursery field-seedlings, for example, were more than double the size of remnant seedlings. In contrast, both the state and federal restorations (Hegg Lake Hill and Runestone respectively) were planted using seeds from production plots from sources within 80 kilometers of the common garden sites and seedlings from these sources, in most cases, had higher germination than remnants seeds but seedling vigor was more similar to the remnants seedlings than too the nursery seedlings.

There may be important consequences to using seeds from production fields (i.e. nursery and restoration sources in this study). Crossing plants from multiple, formerly isolated, remnant populations in propagation fields may produce offspring with hybrid vigor in the first generation when deleterious recessive alleles are masked. However, subsequent generations may experience significant outbreeding depression as co-adapted gene complexes are recombined, which may have long-term consequences on restorations using those seeds (Tallmon et al., 2004; Kramer & Havens, 2009). In addition, seeds produced in production fields are vulnerable to founder effects and unintentional human selection (Lesica & Allendorf, 1999; Hufford & Mazer, 2003; Kramer & Havens, 2009). This can happen both during the seed collection phase and the propagation phase if the genetic diversity of the founding population is low or if seeds are gathered, either during collection or after propagation, from 'good-looking' plants or always at the same time of year. This 'artificial' selection may have important consequences for restoration projects, including the dilution of genes associated with other aspects of performance or in the development of genotypes that might become over-dominant and suppress species diversity (Lesica & Allendorf, 1999).

Restoration seed mixes typically have an over-abundance of warm-season grasses compared to cool-season grass and forb species. These warm-season grasses can suppress the establishment of rare forb species leading to lower species diversity in the restorations (Wilsey, 2010). Grasses have been shown to inhibit forb recruitment by either growing tall and out-competing other species for light and resources (e.g. tall-statured species: *S. nutans* and *A. gerardii*) or by quickly colonizing bare ground with rapidly spreading basal areas and high stem production (e.g. medium and short-statured species: *B. curtipendula*, Wilsey, 2010). The proportion of biomass production from C4 grasses within and among prairies can vary greatly. In studies of local, non-local, and cultivar prairie grass performance, Wilsey (2010) found that cultivars had consistently higher basal areas compared to local remnant sources and Gustafson *et al.* (2004b) found that cultivars were approximately twice as tall and consistently outcompeted plants of other local and non-local remnants. In addition to the competitive advantage, investigators have found that *A. gerardii* cultivars have higher photosynthetic rates than local plants (Skeel & Gibson, 1996). Although cultivars are specifically bred for certain traits (e.g. seed and forage yields, winter survival, high vigor, etc.), it is not impossible that nurseries, like those in this study, use similar methods and consciously or unconsciously subject their propagation fields to selection for greater plant vigor, higher germination, and synchronous phenology. Dominant prairie grasses play an important role in regulating species diversity and restoring ecosystem function. It is important that practitioners do not impede their own efforts by introducing maladapted or over-dominant genotypes to their projects.

Differences in ploidy levels within plant species represent another area of concern. Many of the species used in prairie restorations, including the three in this study, are polyploids and self-

incompatible: *S. nutans* is tetraploid, *B. curtipendula* is also tetraploid but has an extensive and nearly continuous series of aneuploids, and *A. gerardii* is a complex polyploid with two cytotype races (types with different ploidy levels, Gustafson et al., 2004b; Tomas De Pisani, 2004; McKay et al., 2005). These ploidy differences increase the risk that land managers may use inappropriate genetic sources for planting projects. This is because important morphological differences may exist among different ploidy races, including differences in mycorrhizal associations and competitive abilities, and perhaps more importantly, recent studies have revealed that there may also be substantial mating incompatibilities among races (Gustafson et al., 2004a; Gustafson et al., 2004b; Rogers & Montalvo, 2004). If land managers fail to recognize the ploidy races as different ecological and evolutionary entities, they could undermine restoration efforts and potentially have a negative impact on surrounding native tallgrass prairie remnant sites as well.

Traits selected during nursery propagation could directly affect intra- and inter-specific competitive dynamics within a community, and can alter the genetic composition of the local genotype through introgression with the local genotypes (Gustafson et al., 2001). In a genetic study of *A. gerardii* from remnant and restored prairies in Illinois and three commonly used cultivars, Gustafson (2000) found that restored populations were more genetically similar to cultivars than they were to the remnant Illinois populations. They hypothesized that introgression of cultivar genes, through pollen dispersal, into the native Illinois populations was responsible. Rhymer and Simberloff (1996) suggested that such introgression, rather than inbreeding depression, was the larger threat compromising natural ecosystems. Restoration practitioners should be cautious of these issues when using seeds from propagation fields as there may be

serious consequences to both the long-term success of the restoration and the health of any surrounding prairie remnants.

Using seed mixes during restoration

Many have suggested that the use of seed mixtures from multiple sources may be the best option for restoration success (Lesica & Allendorf, 1999; Dolan et al., 2008). They assert that to have the best chance of successful long-term survival, restored populations should reflect the extant variation found in remnants. However, restored sites may suffer from genetic bottlenecks if seed collection is limited, either by the number of source populations or the number reintroductions. Using seed mixtures from multiple local remnant populations has been shown to capture the majority of local genetic diversity while minimizing the risk of founder effects and avoiding introduction of highly maladapted genotypes (Lesica & Allendorf, 1999; Gustafson et al., 2002; Dolan et al., 2008; Bischoff et al., 2010). One notable example in support of seed mixes is the large-scale restoration at Kankakee Sands, Indiana. Comparison among the restoration, on-site seed nursery, and local remnant source populations (within 80 kilometers) revealed that the majority of allozyme variation present in the remnant populations is maintained in restorations (Dolan et al., 2008). In another study, scientists found that remnant Illinois prairie populations were less genetically diverse than the restorations established using seeds from a minimum of two local remnant sources (Gustafson et al., 2002).

Given the concerns about founder effects, preventing introduction of over-dominant or maladapted genotypes, and preserving native prairies from genetic contamination, combined with the possibility that other long-term plant adaptations may exist that were not detected in this study (e.g. resistance to insects, acclimatization to northern Minnesota winters, etc.), my result

support that the use of seed mixes from multiple local seed sources may enhance short-term seedling establishment and long-term success of prairie restorations (Dolan et al., 2008; Bischoff et al., 2010).

To what extent do germination and performance differ among restoration sites?

Germination and survival of field-seedlings, but not plug-seedlings, differed significantly among common garden sites for all species. Common garden site also had a significant influence on plant vigor for *S. nutans* and *B. curtipendula*, but not *A. gerardii*, field-seedlings, and on plug-seedlings of all species. Plug-seedlings of all species and sources (except *S. nutans* from JI Case Hill), were tallest at the B. Mahoney common garden site and most were shortest at Runestone. Likewise, field-seedlings typically had higher germination and were more vigorous at the B. Mahoney common garden site, however this was less consistent among species and sources in field-seedlings. These results suggest that restoration practices can have an important influence on seed germination and seedling performance, and that these effects can be species-specific.

Warm-season grasses have typically been considered to be ecologically equivalent because they are in the same functional group. However, this and other studies have found evidence to suggest that important differences among dominant grass species exist, which may impact restoration success (Silletti & Knapp, 2001). In one important example, researchers comparing *A. gerardii* and *S. nutans* responses to manipulations of nitrogen and water, found that *A. gerardii* was relatively unresponsive to resource limitation but that decreased Nitrogen and water availability significantly reduced leaf-level photosynthesis and stomatal conductance of *S. nutans* plants (Silletti & Knapp, 2001). The finding that *S. nutans* plants may be more sensitive to environmental stress than *A. gerardii* plants, is consistent with the results of this study, in which

common garden site had a significant influence on *S. nutans* seedlings for all analyses, except plug-seedling survival, but only influenced *A. gerardii* field-seedling germination and survival and plug-seedling leaf length, but not leaf count, two months after planting. The existence of such important differences among three 'ecologically similar' prairie grass species suggests that practitioners should be cautious when generalizing the response of one species to a restoration practice to those of other "similar" species in prairie ecosystems.

Does the use of plugs versus seeds affect seedling establishment and growth in restorations?

As discussed, the effect common garden site and seed source on seed germination and seedling performance differed between plug-seedlings and field-seedlings and varied among species. In addition, planting method had a strong influence on overall plant establishment. Seed germination in the growth chambers was 3-12 times higher than it was for seeds directly sown into the common garden sites. Plug-seedling mortality pre-planting was high (50-82%), however, mortality of both plug and field-seedlings post-planting was extremely low (> 1% for field-seedlings, > 15% for plug-seedlings). Overall, plug-seedling establishment was 3-6 times higher than field-seedling establishment. The high survival of seedlings post-planting suggests that germination is likely to be critical stage in restoration establishment (Middleton et al., 2010; Seifert & Fischer, 2010; Yurkonis et al., 2010a; Yurkonis et al., 2010b). However, the use of transplanted seedlings (i.e. plugs) in restoration is often logistically and economically unrealistic. Therefore, due to the low germination in field-sown seeds, restorations may require multiple reintroductions in order to be successful (Middleton et al., 2010).

Despite land managers best efforts most restorations do have lower plant diversity than representative of native remnants. The reason for this is not fully understood, however, a key

component is probably that the seed mixes typically used during restoration have an over-abundance of warm-season grasses compared to cool-season grass and forb species (Wilsey, 2010). While multiple studies have found that the early establishment of natives can inhibit exotic invasion (Seifert & Fischer, 2010; Stevens & Fehmi, 2011). In an investigation into the effect of restoration method on plant community structure, Middleton *et al.* (2010) found a negative correlation between native plant diversity and the establishment of weedy exotics. In addition, Middleton *et al.* (2010) found that the use of transplanted seedlings (i.e. plug-seedlings) over the first four years of restoration resulted in greater species richness and diversity. In light of these results combined with the higher germination and survival of plug-seedlings that were found this study, it may be advisable for managers to consider supplementing seeded restorations with plug-seedlings, particularly forbs. This may help increase over-all diversity of the site, thus reducing invisibility by exotics, while minimizing the costs related to low germination in field planted seeds.

The map displays the study area in the Kensington area. Key features include:

- Roads:** Tower Hill Rd, Westridge La, Borelder Dr, Tower Rd, Pleasant Rd, Beacon Rd, Wally Lake Rd, County Rd 103, W of Anderson, Anenison, Solem Lake Rd, County Rd 96, Mellow La, Grove La, Roland Lake Rd, Wickersburg Rd, Unity Dr, and Stettinson Prairie.
- Lakes:** Red Rock Lake, Wally Lake, Eng Lake, and Roland Lake.
- Landmarks:** Farm, Transplant plot, Tower, Nessman, B.T.G., South of Golf Course, Golf Course, North of Golf Course, Liatri's Hill, Krusemark, Landfill, and East of Town Hall.
- Recruitment Sites:** Recruit#1, Recruit#2, Recruit#3, Recruit#4, Recruit#5, Recruit#6, Recruit#7, Recruit#8, Recruit#9, and Recruit#10.
- Grid System:** Numbers 1, 2, 3, 4 and letters A, B, C, D are overlaid on the map.

Three experimental common garden plots were planted at the three restoration locations using seeds from all (remnant, restoration, and nursery) seed sources.

- 45 - 80 km

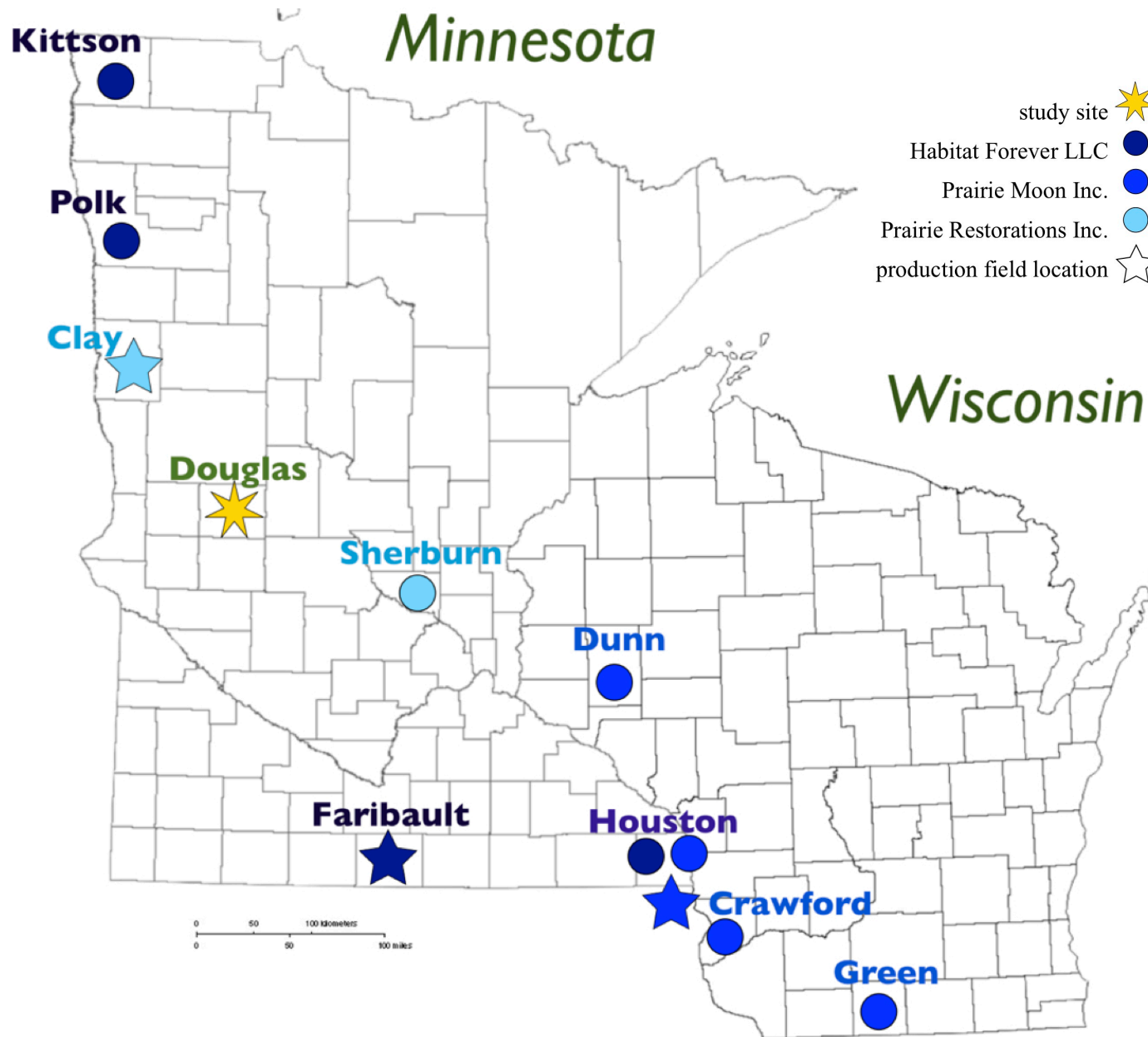


Figure 2: Map of seed collection and propagation sites for three Minnesota prairie seed nurseries. All propagation fields and collection locations are more than 160km from study area in Douglas County, MN.

Figure 3: Germination of *A. gerardii*, *S. nutans*, and *B. curtipendula* field-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed one month after planting into three common garden plots. Germination was analyzed with generalized linear models assuming a quasibinomial error distribution. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

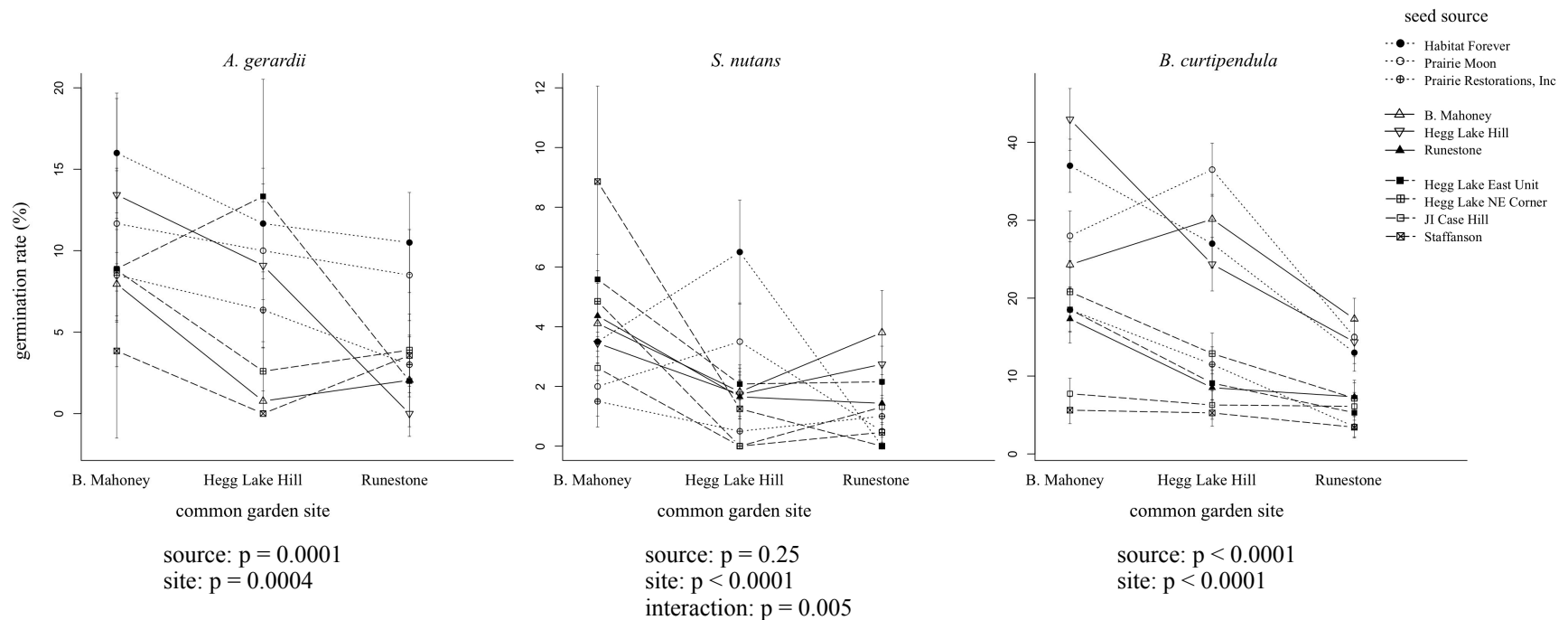


Figure 4: Survival of *A. gerardii*, *S. nutans*, and *B. curtipendula* field-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed two months after planting into three common garden plots. Survival was analyzed with generalized linear models assuming a quasibinomial error distribution. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

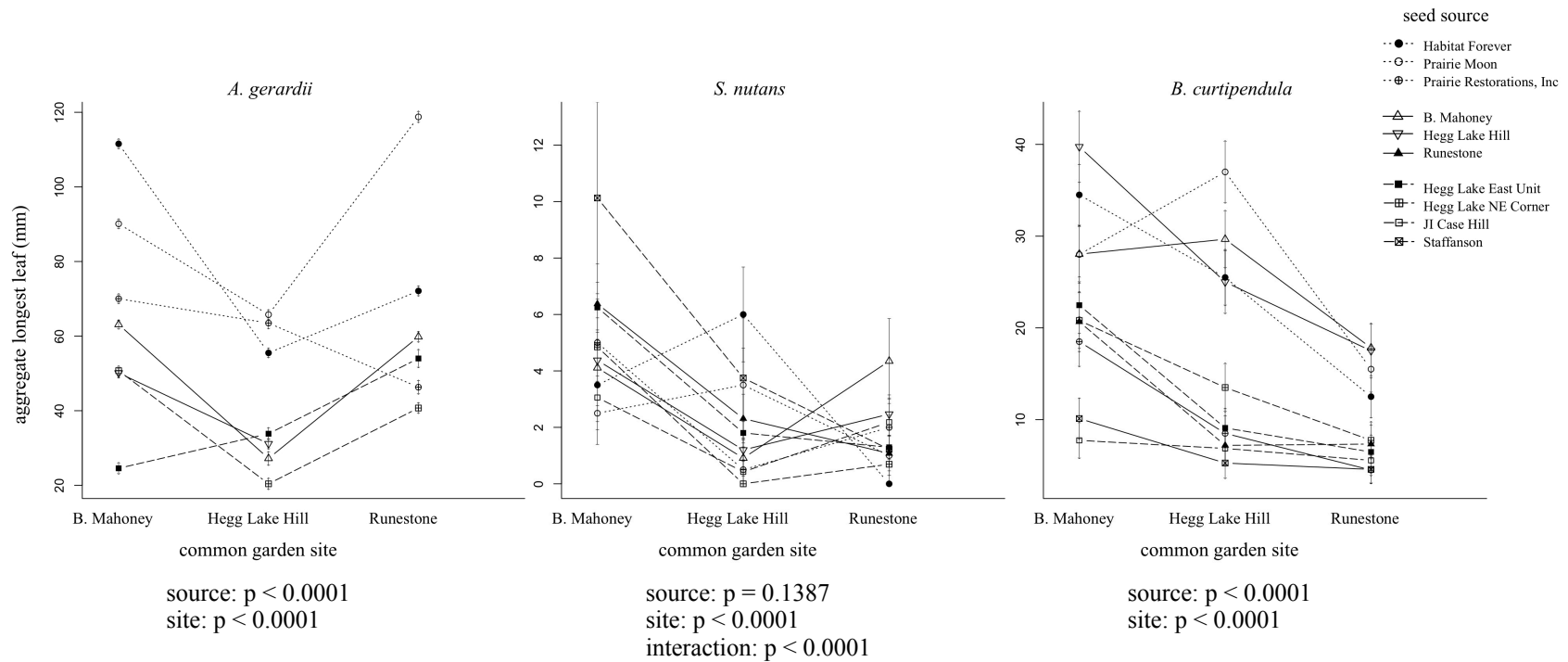


Figure 6: Aggregate longest leaf of *A. gerardii*, *S. nutans*, and *B. curtispindula* field-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed one month after planting into three common garden plots. Log transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection of field-seedling vigor. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

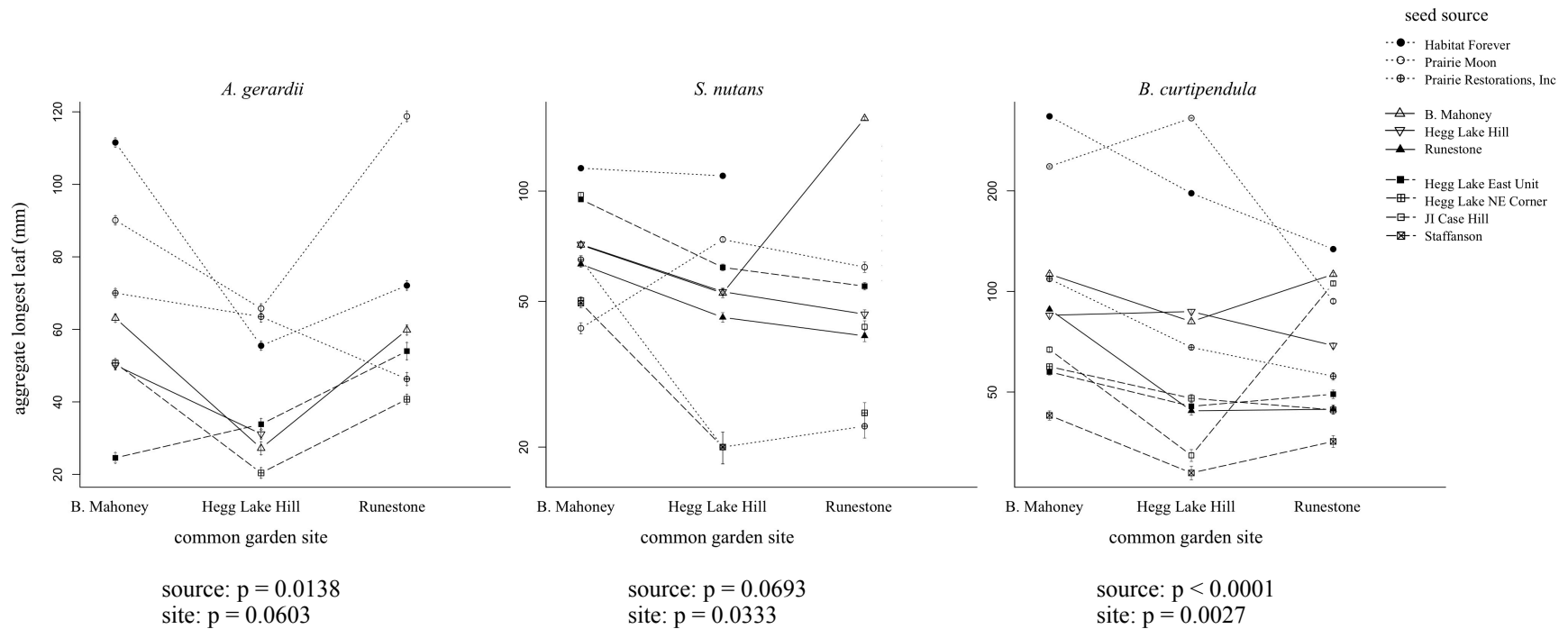


Figure 7: Aggregate longest leaf of *A. gerardii*, *S. nutans*, and *B. curtipendula* field-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed two months after planting into three common garden plots. Log transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection of field-seedling vigor. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

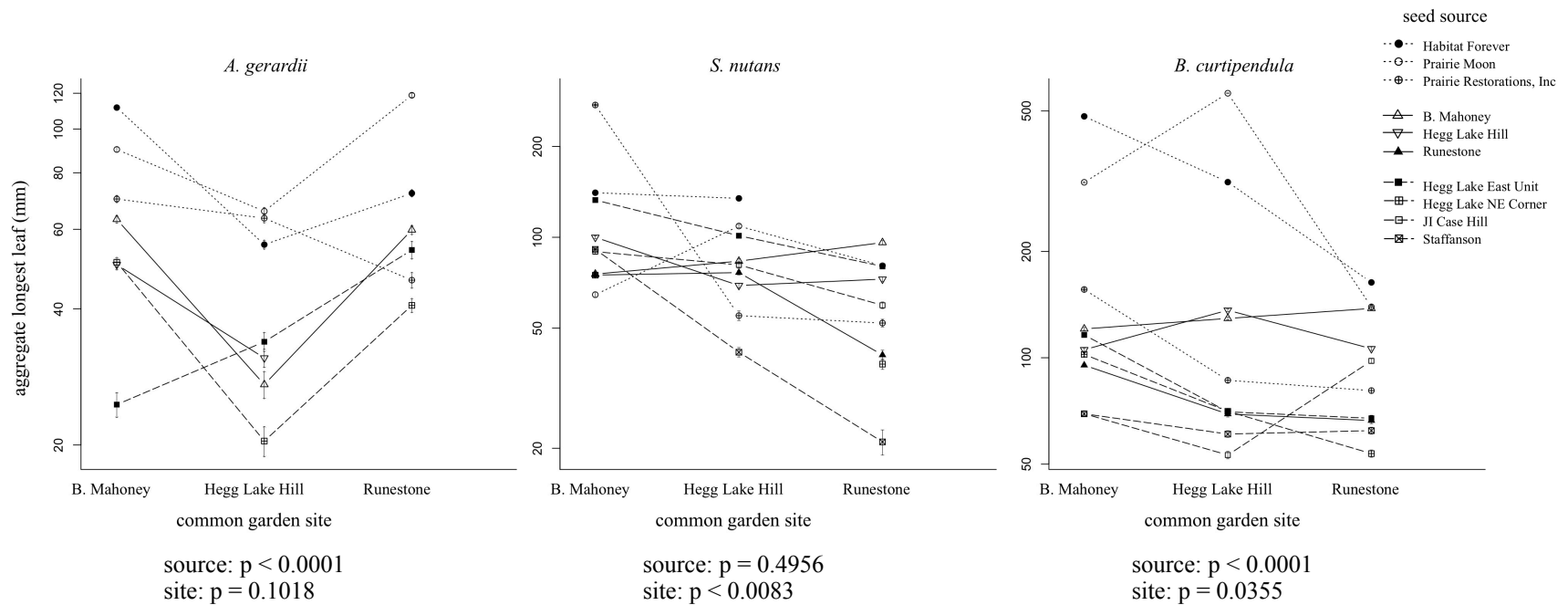


Figure 8: Mean longest leaf of *A. gerardii*, *S. nutans*, and *B. curtipendula* plug-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed two months after planting into three common garden plots. Plug-seedling vigor (longest leaf height in centimeters) was analyzed with a linear model. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

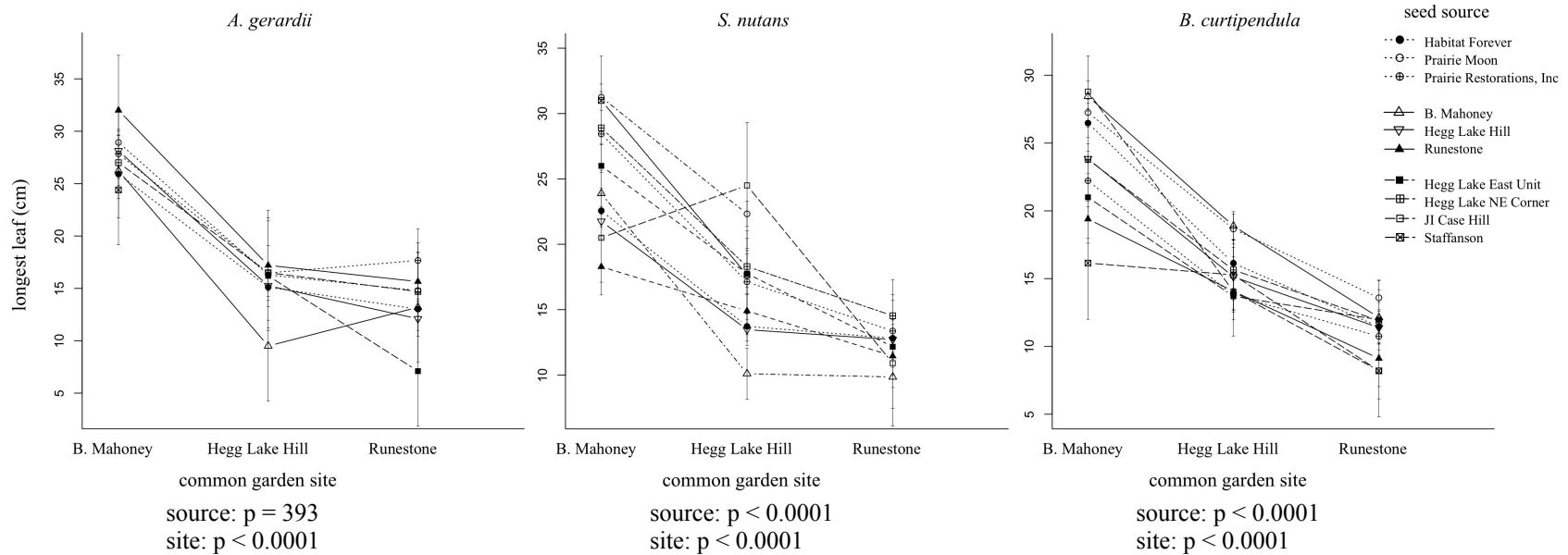


Figure 9: Mean leaf count of *A. gerardii*, *S. nutans*, and *B. curtispindula* plug-seedlings from ten sources (4 remnant, 3 restoration, 3 nursery), assessed two months after planting into three common garden plots. Plug-seedling vigor (leaf count) was analyzed with generalized linear models assuming a poisson error distribution. Circles denote nursery seed sources (Habitat Forever, Prairie Moon, Prairie Restorations Inc.); squares denote remnant seed sources (Hegg Lake East Unit, Hegg Lake NE Corner, JI Case Hill, Staffanson); triangles denote restoration seed sources (B. Mahoney, Hegg Lake Hill WMA, Runestone WPA).

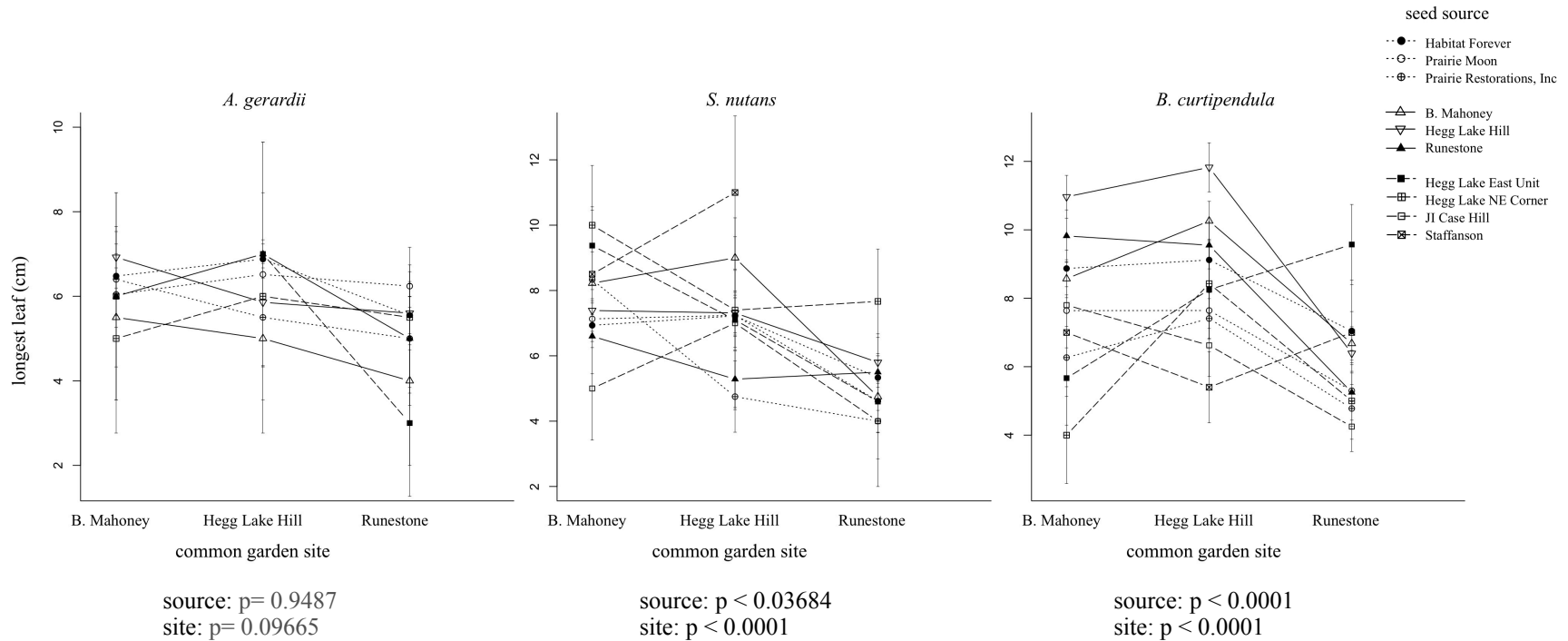


Table 1: Seed sources and sampling quantities for each *A. gerardii*, *S. nutans*, and *B. curtipendula* seeds.

Collection Source	Location Co., State	Distance (km)			<i>A. gerardii</i>					<i>S. nutans</i>					<i>B. curtipendula</i>				
<i>Remnants</i>	Douglas County, MN	rune	hlh	bm	maternal lines		seeds used			maternal lines		seeds used			maternal lines		seeds used		
					collected	used	GC	field	total	collected	used	GC	field	total	collected	used	GC	field	total
Staffanson Prairie Reserve	45°81'05"N 95°75'04"W, 45-ha	7.02	7.12	5.37	50	50	61	82	143	50	50	144	241	385	50	30	250	524	774
JI Case Hill	45°85'98"N 95°64'19"W, 2.3-ha	6.47	8.44	4.56	29	29	3	2	5	50	50	135	693	828	44	30	266	536	802
Hegg Lake East Unit	45°76'81"N 95°67'38"W, 5.7-ha	1.88	0.5	4.6	50	20	92	146	238	50	50	380	2254	2634	50	30	268	524	792
Hegg Lake NE Corner	45°76'69"N 95°65'87"W, 2.5-ha	1.67	0.82	4.6	50	50	241	467	708	50	25	191	1298	1489	50	30	269	503	772
<i>Restorations</i>	Douglas County, MN																		
Runestone WPA (rune)	45°80'31"N 95°65'60"W, 8.2-ha	-	2.01	3.21	50	25	91	155	246	50	37	273	903	1176	50	30	257	453	710
	Source: Otter Tail County, MN	80 km NW																	
Hegg Lake Hill (hlh)	45°76'64"N 95°67'65"W, 2.4-ha	2.01	-	4.4	50	25	151	203	354	50	49	430	2252	2682	50	30	275	468	743
	Sources: Otter Tail County, MN; Stevens County, MN	80 km NW; 45 km SW																	
B. Mahoney's Restoration (bm)	45°79'94"N 95°68'34"W, 6-ha	3.21	4.4	-	50	39	302	1172	1474	50	25	195	656	851	50	30	249	615	864
	Source: Douglas County	50 km NE																	
<i>Nurseries</i>					purchased		seeds used			purchased		seeds used			purchased		seeds used		
							GC	field	total			GC	field	total <td></td> <td></td> <th>GC</th> <th>field</th> <th>total</th>			GC	field	total
Prairie Moon Nursery, Inc.	Dunn County, WI	340 km SE			11b		270	600	870										
	Green County, WI	685 km SE								11b		270	600	870					
	Crawford County, WI; Houston County, MN	550 km SE; 470 km SE													11b		270	600	870
Habitat Forever, LLC	Polk County, MN	250 km NW			11b		270	600	870										
	Kittson County, MN	370 km NW								11b		270	600	870					
	Houston County, MN	470 km SE													11b		270	600	870
Prairie Restorations, Inc.	Sherburne County, MN	160 km SE			11b		270	600	870	11b		270	600	870	11b		270	600	870
Total:							1,751	4027	5,778			2,558	10097	12,655			2,644	5423	8,067

Table 2: Summary of experimental results for *A. gerardii*, *S. nutans*, and *B. curtipendula* field and plug-seedling germination, survival until two months after planting and seedling vigor two months after planting (field-seedlings: aggregate longest leaf, plug-seedlings: longest leaf).

		germination		survival (2 months after planting)		vigor (longest leaf, 2 months after planting)	
		source	site	source	site	source	site
<i>A. gerardii</i>	plug-seedlings	***	-	***	NS	NS	***
	field-seedlings	***	**	***	***	***	NS
<i>S. nutans</i>	plug-seedlings	***	-	***	NS	***	***
	field-seedlings	NS interaction ♦ ***		NS	***	NS	*
<i>B. curtipendula</i>	plug-seedlings	***	-	***	NS	***	***
	field-seedlings	***	***	***	***	***	♦

Significance codes: $p < 0.0001$ '***' 0.001 '**' 0.01 '*' 0.05 '♦' 0.1 'NS'

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APPENDIX

Table A1. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Andropogon gerardii* field-seedling germination (A), survival until two months after planting (B), and vigor one (C) and two months after planting (D).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>			
sourceType:source	5	25.85	0.0429
sourceType:site	4	13.95	0.1836
sourceType	2	39.07	0.0001
site	2	33.76	0.0004
<i>maximal model 2: site + source + site:source</i>			
site:source	14	35.65	0.2255
source	7	64.57	0.0001
site	2	33.76	0.0004
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	5	29.04	0.0166
sourceType:site	4	14.58	0.1361
sourceType	2	34.68	0.0003
site	2	46.71	<0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	14	40.26	0.1013
source	7	63.27	<0.0001
site	2	46.71	<0.0001
(C) Vigor (1 month, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	4	1.18	0.8340
sourceType:site	4	0.52	0.9565
sourceType	2	11.87	0.0007
site	2	4.95	0.0443
<i>maximal model 2: site + source + site:source</i>			
site:source	11	3.71	0.9519
source	6	13.30	0.0138
site	2	4.54	0.0603
(D) Vigor (2 months, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	4	2.73	0.3092
sourceType:site	4	1.09	0.7483
sourceType	2	21.11	< 0.0001
site	2	2.87	0.0805
<i>maximal model 2: site + source + site:source</i>			
site:source	11	6.59	0.3739
source	6	23.77	< 0.0001
site	2	2.58	0.1018

Germination (A) and survival (B) were analyzed with a generalized linear model, assuming a quasibinomial error distribution. I used log transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection of field-seedling vigor one (C) and two months after planting (D). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.

Table A2. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Sorghastrum nutans* field-seedling germination (A), survival until two months after planting (B), and vigor one (C) and two months after planting (D).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>			
sourceType:source	7	22.78	0.1420
sourceType:site	4	33.14	0.0051
sourceType	2	1.72	0.6885
site	2	47.79	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	18	65.44	0.0132
source	9	24.61	0.2461
site	2	47.10	< 0.0001
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	7	13.23	0.5689
sourceType:site	4	21.43	0.0592
sourceType	2	0.37	0.9246
site	2	83.89	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	18	62.39	< 0.0001
source	9	13.57	0.1387
site	2	83.64	< 0.0001
(C) Vigor (1 month, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	9.39	0.0379
sourceType:site	4	3.42	0.2244
sourceType	2	0.62	0.6209
site	2	4.26	0.0333
<i>maximal model 2: site + source + site:source</i>			
site:source	14	10.46	0.2447
source	9	10.01	0.0693
site	2	4.26	0.0333
(D) Vigor (2 months, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	6.92	0.0533
sourceType:site	4	1.23	0.6437
sourceType	2	1.56	0.2184
site	2	4.79	0.0083
<i>maximal model 2: site + source + site:source</i>			
site:source	16	6.89	0.5962
source	9	8.48	0.4956
site	2	4.79	0.0083

Germination (A) and survival (B) were analyzed with a generalized linear model, assuming a quasibinomial error distribution. I used log transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection of field-seedling vigor one (C) and two months after planting (D). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.

Table A3. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Bouteloua curtipendula* field-seedling germination (A), survival until two months after planting (B), and vigor one (C) and two months after planting (D).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>			
sourceType:source	7	137.56	< 0.0001
sourceType:site	4	6.96	0.5145
sourceType	2	151.24	< 0.0001
site	2	122.81	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	18	42.75	0.3295
source	9	288.58	< 0.0001
site	2	122.81	< 0.0001
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	7	134.61	< 0.0001
sourceType:site	4	7.97	0.4431
sourceType	2	125.34	< 0.0001
site	2	119.99	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	18	40.59	0.3849
source	9	259.80	< 0.0001
site	2	119.99	< 0.0001
(C) Vigor (1 month, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	24.79	< 0.0001
sourceType:site	4	6.67	0.0353
sourceType	2	61.69	< 0.0001
site	2	4.66	0.0268
<i>maximal model 2: site + source + site:source</i>			
site:source	18	15.98	0.1309
source	9	84.65	< 0.0001
site	2	7.84	0.0027
(D) Vigor (2 months, aggregate longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	25.99	< 0.0001
sourceType:site	4	7.87	0.0095
sourceType	2	53.58	< 0.0001
site	2	3.86	0.0363
<i>maximal model 2: site + source + site:source</i>			
site:source	18	17.18	0.0441
source	9	79.08	< 0.0001
site	2	3.86	0.0355

Germination (A) and survival (B) were analyzed with a generalized linear model, assuming a quasibinomial error distribution. I used log transformed aggregate leaf height (sum of the heights of the longest leaves of all seedlings from each maternal line in millimeters) as the response for linear model selection of field-seedling vigor one (C) and two months after planting (D). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.

Table A4. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Andropogon gerardii* plug-seedling germination (A), survival until two months after planting (B), and vigor two months after planting (C).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: sourceType + sourceType:source</i>			
sourceType:source	6	1,063.80	< 0.0001
sourceType	2	1,253.50	< 0.0001
<i>maximal model 2: source</i>			
source	8	189.64	< 0.0001
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	6	3.74	0.7117
sourceType:site	4	0.61	0.9622
sourceType	2	39.63	< 0.0001
site	2	2.82	0.2699
<i>maximal model 2: site + source + site:source</i>			
site:source	14	5.65	0.9747
source	8	41.54	< 0.0001
site	2	2.65	0.2660
(C) Vigor (2 months, longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	6	260.60	0.1422
sourceType:site	4	28.81	0.9005
sourceType	2	14.13	0.7690
site	2	8,174.80	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	13	134.12	0.9765
source	8	533.59	0.3930
site	2	8,174.80	< 0.0001

Germination (A) was analyzed with generalized linear models assuming a quasibinomial error distribution. Survival until 2 months after planting (B) was analyzed with generalized linear models with binomial error distributions. Longest leaf height (centimeters) was the response for linear model selection of plug-seedling vigor two months after planting (C). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.

Table A5. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Sorghastrum nutans* plug-seedling germination (A), survival until two months after planting (B), and vigor two months after planting (C).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: sourceType + sourceType:source</i>			
sourceType:source	7		< 0.0001
sourceType	2		< 0.0001
<i>maximal model 2: source</i>			
source	9		< 0.0001
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	7	5.74	0.5705
sourceType:site	4	2.92	0.5710
sourceType	2	95.77	< 0.0001
site	2	2.59	0.2738
<i>maximal model 2: site + source + site:source</i>			
site:source	17	16.56	0.4843
source	9	101.37	< 0.0001
site	2	2.27	0.0321
(C) Vigor (2 months, longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	1,525.40	< 0.0001
sourceType:site	4	79.49	0.5034
sourceType	2	1,259.70	< 0.0001
site	2	5,753.20	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	17	524.51	0.1733
source	9	2,808.70	< 0.0001
site	2	5,692.50	< 0.0001

Germination (A) was analyzed with generalized linear models assuming a quasibinomial error distribution. Survival until 2 months after planting (B) was analyzed with generalized linear models with binomial error distributions. Longest leaf height (centimeters) was the response for linear model selection of plug-seedling vigor two months after planting (C). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.

Table A6. Likelihood ratio tests for stepwise model simplification using backward elimination for analyses of *Bouteloua curtipendula* plug-seedling germination (A), survival until two months after planting (B), and vigor two months after planting (C).

(A) Germination			
Focal term (interaction or factor)	df	Deviance	P
<i>maximal model 1: sourceType + sourceType:source</i>			
sourceType:source	7	790.92	< 0.0001
sourceType	2	1,129.60	< 0.0001
<i>maximal model 2: source</i>			
source	9	1,920.50	< 0.0001
(B) Survival (2 months)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Deviance	P
sourceType:source	7	126.74	< 0.0001
sourceType:site	4	0.45	0.9785
sourceType	2	31.17	< 0.0001
site	2	1.71	0.4251
<i>maximal model 2: site + source + site:source</i>			
site:source	18	14.75	0.6792
source	9	158.61	< 0.0001
site	2	1.71	0.4351
(C) Vigor (2 months, longest leaf)			
<i>maximal model 1: site + sourceType + site:sourceType + sourceType:source</i>	df	Sum of sq	P
sourceType:source	7	1,683.10	< 0.0001
sourceType:site	4	32.86	0.9178
sourceType	2	178.04	0.0947
site	2	15,410.00	< 0.0001
<i>maximal model 2: site + source + site:source</i>			
site:source	18	651.88	0.4007
source	9	1,871.00	< 0.0001
site	2	14,639.00	< 0.0001

Germination (A) was analyzed with generalized linear models assuming a quasibinomial error distribution. Survival until 2 months after planting (B) was analyzed with generalized linear models with binomial error distributions. Longest leaf height (centimeters) was the response for linear model selection of plug-seedling vigor two months after planting (C). *P* values are for the F test of the null hypothesis that a model simplified by excluding the focal term is not significantly different from a model including the focal term. Two maximal models were tested for each response, (1) where the ten seed sources were nested within source type and (2) where source type was not included. The models included main effects of common garden site location (site), source (source), and seed source type, remnant, restoration, and nursery (sourceType). Significant values are in bold.