

Seed Sourcing for Resilient Reconstructed Prairies

There are tremendous challenges to creating guidelines for seed translocation. Determining the ecologically appropriate distance to move plant materials for reintroduction is a continual subject of debate among restoration ecologists (Herman et al. 2014). Often the factors that affect plant genetics have little to do with geographic distance, and more to do with environmental similarity. Limiting the distance of seed translocation is therefore inadequate. Similarly, the scope of seed transfer zones are likely to differ between species depending on biological traits such as pollination and seed dispersal mechanisms. There are not simple guidelines to follow.

Despite these challenges of seed sourcing, large volumes of tallgrass prairie seed are needed for planned reconstructions. Seed needs to be available, cost-effective, and genetically diverse enough to sustain the prairie ecosystem through time. Determining the best source for prairie reconstruction seed can be challenging, with practitioners often needing to balance a variety of factors such as species availability, origin, and cost. The stakes are high with the cost of seed potentially reaching \$750 per acre or more, one cannot risk a seeding failure due to improperly sourced seed. The objective of this guide is to help prairie reconstruction practitioners better understand the various factors involved with sourcing seed.

Plant Genetic Diversity

One of the goals of prairie reconstruction is to maintain plant genetic diversity. Plant genetic diversity is likely to support a functioning ecosystem through improved establishment, increased resistance to disease and pest pressure, and resilience during extreme climatic events such as floods and drought. Similarly, genetic diversity provides a foundation upon which ecosystems have the ability to adapt to changing climatic regimes. Plant genetic diversity has the potential to support a greater diversity of other organisms that rely on plants for survival such as animals and fungi. Some evidence suggests that greater genetic diversity in the plant community improves nutrient retention and ecosystem productivity (Basey et al. 2015). Temperature and precipitation are environmental variables that are often associated with genetic divergence among populations of herbaceous plants (Bower et al. 2014), including big bluestem, *Andropogon gerardii* (Gray et al. 2014). Ecoregions (delimited based on climate, vegetation, geology, soils, and hydrology) may serve as a basis for seed transfer zones for historically widespread species (Miller et al. 2011). Understanding differences in plant genetic diversity is at the foundation of determining the best sources of seed for reconstructions. Genetic variability between and within populations is not well understood for most prairie species, but some inferences can be made from other systems.

Seed Sourcing Options – Mix or Match?

One of the most challenging questions is ‘how far should we move seed for prairie reconstructions?’ A variety of choices are available when sourcing seed for reconstructed prairies. Below are several potential categories of seed sourcing options, and the potential positive and negative impacts of the strategy on plant genetic diversity. Biologically, the goal is to strike a balance between avoiding inbreeding depression by moving seed only a short distance, and avoiding outbreeding depression by moving seed too far; the match or mix conundrum (Hufford et

al. 2012). These are not necessarily mutually exclusive categories, and not all plants respond to the strategies in the same manner.

Local Seed Source - Match

A commonly suggested method for sourcing seed for prairie reconstruction is to use the most local (geographically close) seed available. The idea is that local seed will be best adapted to local environmental conditions, sometimes termed the 'local is best' approach or 'home-site advantage', although 'local' is typically not defined or differs widely between studies (Herman et al. 2014). Despite this prevailing view, there is not a strong scientific basis for locally sourced seed being the best (Broadhurst et al. 2008). One of the main challenges with this approach is in obtaining sufficient volumes for the growing demand, and limited supply of tallgrass prairie seed (Broadhurst et al. 2008), especially at the maximum seed movement distances cited in some studies (<12 miles; Krauss and Koch 2004). Additionally, using only very local seed could cause inbreeding depression (Hufford and Mazer 2003) if small, local population harbor low genetic diversity. For example, a high degrees of relatedness within populations of purple coneflower – *Echinacea angustifolia* (Wagenius et al. 2010) is likely to lead to inbreeding depression in this species under the local is best approach. However, research in prairie systems suggest that small populations are not necessarily prone to low genetic diversity, or inbreeding depression in big bluestem, Indian grass, and purple prairie clover (Gustafson et al. 1999, 2002), prairie cordgrass and spotted joe-pye weed (Moncada et al. 2007), switchgrass (Mutegi et al. 2014), and butterfly milkweed (Ploegstra et al. 2015).

Seed Source Zones - Mixing

Some states have adopted seed source zones where seed from multiple populations within a zone are mixed together prior to distribution and planting (Houseal and Smith 2000). This approach allows for a greater potential for self-sorting of those seeds that are best suited to the environmental conditions of the planting site compared with using exclusively locally sourced seed. Greater genetic diversity increases the chance that the individuals best suited for that particular habitat will establish (Houseal and Smith 2000). Broadening the geographic scope may result in more sources of higher quality seed resulting in more successful reconstructions (Broadhurst et al. 2008). Mixing seeds from multiple populations supported higher species diversity compared with reconstructions that were planted using only local ecotype seed (Wilson et al. 2016). Mixing is thought to facilitate outcrossing by mimicking long-distance gene flow, and mitigate inbreeding depression in a now fragmented landscape in which plants may not be dispersing as far as they had in the past. Another potential benefit of mixing populations is to predictively select seed from environments that might match the future climate of the site based on models of global climate change (Havens et al. 2015). Mixing seed from multiple sources seems to support the goal of restoration genetics by creating resilience communities, but care still needs to be taken to avoid outbreeding depression caused by moving seed too far from the source (Hufford et al. 2012). Some suggest that populations should only be mixed when there is a documented concern of inbreeding depression (Vander Mijnsbrugge et al. 2010).

Production Farms

Locally sourced seed is often grown on production farms prior to distribution for restoration projects. Producers create large plots to provide sufficient quantities to fulfill the supply demand. Large quantities of seed can be grown and supplied to the conservation community using this strategy. Through the process of collecting seed,

growing that seed in production plots, and using farm-sourced seed in restorations, there is potential for unintentional genetic selection during each step in the process (Espeland et al. 2017). This sequence is likely to lead to decreased genetic diversity available for restorations even through the course of a few growing seasons (Vander Mijnsbrugge et al. 2010). In particular, on-farm production practices are likely to unintentionally select for certain plant characteristics such as flowering time, seed retention (e.g., seeds staying attached to the plant), rapid germination, and rapid growth (Espeland et al. 2017). These selective forces on the farm ultimately influence the genetic diversity of restorations unless steps are taken to mitigate inbreeding depression caused by the process of propagation. The first step is to maximize the genetic diversity of the seed that is collected for production plots (see section on Factors to Consider When Collecting Seed). Attempts to grow seed on farms in similar situations found in restorations (e.g., polyculture, diverse soil types, and variable microclimates) are likely to support greater plant genetic diversity (Espeland et al. 2017).

Cultivars

Declining phenotypic variation in cultivated grasses such as big bluestem can happen in just a few generations of production fields. (Law and Anderson 1940). Prairie grass cultivars can retain similar levels of genetic diversity within populations as compared with remnant populations (Gustafson et al. 2004a, Selbo and Snow 2005, Baer et al. 2014), but can still differ genetically from local populations (Mutegi et al. 2014). Some switchgrass cultivars have been shown to have reduced genetic variation within populations, suggesting genetic bottlenecks (Mutegi et al. 2014). Cultivars such as big bluestem, switchgrass, and little bluestem have been shown to exhibit superior plant performance physiologically, in both the field and greenhouses compared with non-cultivars suggesting that these species may have a competitive advantage potentially leading to dominance in reconstructions (Lambert et al. 2011). The prevailing viewpoint that cultivars can cause dominance in reconstructions has been challenged by a few studies which suggest that the cultivars do not outcompete subordinate species or have greater biomass than local ecotype plants (Wilsey 2010, Baer et al. 2014).

Biological Traits Influence Plant Genetic Diversity

Certain functional groups of plants may retain or lose historical levels genetic diversity under the pressures of habitat loss and fragmentation due to increased likelihood of mating between close relatives. There is a lack of scientific understanding about how different plant functional traits (e.g., wind- vs. insect-pollinated, outcrossing vs. self-compatible, polyploid vs. diploid) might affect transplant zone size. Wind-pollinated and outcrossing species tend to have the most genetic homogeneity between populations; insect-pollinated and outcrossing species have intermediate levels of between-population genetic diversity; and insect-pollinated and self-compatible species have the highest genetic diversity (Durka et al. 2016). Outcrossing species are likely to have a higher potential of inbreeding depression caused by fragmentation, compared with self-compatible species (McKay et al. 2005). Big bluestem and Indian grass have high levels of genetic diversity within even small populations, and this may be due to their life history traits (i.e., mating systems, dispersal strategies, reproduction methods) (Gustafson et al. 2004b). Purple prairie clover – *Dalea purpurea* (insect-pollinated and outcrossed) in the highly fragmented landscape of Illinois had low genetic diversity within populations (Gustafson et al. 2002). Yellow sundrop – *Calylophus serrulatus*, another insect-pollinated forb, exhibits outbreeding depression at a scale of only 12 miles (Heiser and Shaw 2006). Species that self-pollinate or are clonal may require smaller seed transfer zones than outcrossing species.

Factors to Consider When Collecting Seed

Several seed collection guidelines can help to support sufficient plant genetic diversity on production farms and restoration plantings. Collecting seed from large population sizes is important, as large populations typically have greater genetic diversity (Basey et al. 2015). This includes collecting seed from multiple sites in the same seed transfer zone (e.g., county) (Espeland et al. 2017). Consider collecting seed from across the entire site, including edges, depressions, and ridges to capture as much genetic variation as possible (Basey et al. 2015). Recent research supports harvesting seed from ‘bad’ sites and ‘bad’ years in order to collect seed that may be able to withstand more dramatic environmental conditions as predicted by models of global climate change (Havens et al. 2015). Making multiple collections from the same population across the seed harvest period is likely to capture greater genetic diversity compared with a single sample in time (Espeland et al. 2017). Harvesting seed from remnant prairies should only be conducted on a site every 3-5 years to avoid damage to short-lived species due to overharvesting (Meissen et al. 2015).

Glossary

Cultivars – seed from plants that have been artificially selected for particular traits, typically rapid growth rate.

Diploid – two sets of chromosomes, one from each parent.

Genetic drift – decreases in genetic diversity due to sampling a portion of the population.

Inbreeding depression – low genetic diversity and fitness due to crossing of related individuals.

Local ecotype – plant materials that have originated from a specific geographical area, and are often presumed to be adapted to the local environmental conditions.

Outbreeding depression – when distantly related plants cross and result in progeny with low fitness.

Outcrossing – a fertilization strategy used by plants requiring pollen from unrelated plants.

Polyloid – more than two sets of chromosomes.

Self-compatible – a fertilization strategy used by plants where self-fertilization is possible.

Draft March 13, 2018

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References Cited

Baer, S. G., D. J. Gibson, D. J. Gustafson, A. M. Benscoter, L. K. Reed, R. E. Campbell, R. P. Klopff, J. E. Willand, and B. R. Wodika. 2014. No effect of seed source on multiple aspects of ecosystem functioning during ecological restoration: Cultivars compared to local ecotypes of dominant grasses. *Evolutionary Applications* 7:323–335.

Basey, A. C., J. B. Fant, and A. T. Kramer. 2015. Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal* 16:37–53.

Bower, A., J. B. St. Clair, and V. Erickson. 2014. Generalized provisional seed zones for native plants. *Ecological*

Applications 24:913–919.

- Broadhurst, L. M., A. Lowe, D. J. Coates, S. A. Cunningham, M. McDonald, P. A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications* 1:587–597.
- Durka, W., S. G. Michalski, K. W. Berendzen, O. Bossdorf, A. Bucharova, J. M. Hermann, N. Hölzel, and J. Kollmann. 2016. Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration. *Journal of Applied Ecology* 54:116–126.
- Espeland, E. K., N. C. Emery, K. L. Mercer, S. A. Woolbright, K. M. Kettenring, P. Gepts, and J. R. Etterson. 2017. Evolution of plant materials for ecological restoration: insights from the applied and basic literature. *Journal of Applied Ecology* 54:102–115.
- Gray, M. M., P. St. Amand, N. M. Bello, M. B. Galliard, M. Knapp, K. A. Garrett, T. J. Morgan, S. G. Baer, B. R. Maricle, E. D. Akhunov, and L. C. Johnson. 2014. Ecotypes of an ecologically dominant prairie grass (*Andropogon gerardii*) exhibit genetic divergence across the U.S. Midwest grasslands' environmental gradient. *Molecular Ecology* 23:6011–6028.
- Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 1999. Random amplified polymorphic DNA variation among remnant big bluestem (*Andropogon gerardii* Vitman) populations from Arkansas' Grand Prairie. *Molecular Ecology* 8:1693–1701.
- Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2002. Genetic diversity and competitive abilities of *Dalea purpurea* (Fabaceae) from remnant and restored grasslands. *International Journal of Plant Sciences* 163:979–990.
- Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2004a. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology* 18:451–457.
- Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2004b. Conservation genetics of two co-dominant grass species in an endangered grassland ecosystem. *Journal of Applied Ecology* 41:389–397.
- Havens, K., P. Vitt, S. Still, A. T. Kramer, J. B. Fant, and K. Schatz. 2015. Seed sourcing for restoration in an era of climate change. *Natural Areas Journal* 35:122–133.
- Heiser, D. A., and R. G. Shaw. 2006. The fitness effects of outcrossing in *Calylophus serrulatus*, a permanent translocation heterozygote. *Evolution* 60:64–76.
- Herman, B., S. Packard, C. Pollack, G. Houseal, C. O'Leary, J. Fant, A. Derby Lewis, S. Wagenius, D. Gustafson, K. Hufford, B. Allison, K. Shaw, S. Haines, and C. Daniels. 2014. Decisions...decisions...how to source plant material for native plant restoration projects. *Ecological Restoration* 32:236–239.
- Houseal, G., and D. Smith. 2000. Source-identified seed : The Iowa roadside experience. *Ecological Restoration* 18:173–183.
- Hufford, K. M., S. L. Krauss, and E. J. Veneklaas. 2012. Inbreeding and outbreeding depression in *Stylidium hispidum*: Implications for mixing seed sources for ecological restoration. *Ecology and Evolution* 2:2262–2273.
- Hufford, K. M., and S. J. Mazer. 2003. Plant ecotypes: Genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18:147–155.

- Krauss, S. L., and J. M. Koch. 2004. Rapid genetic delineation of provenance for plant community restoration. *Journal of Applied Ecology* 41:1162–1173.
- Lambert, A. M., S. G. Baer, and D. J. Gibson. 2011. Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: Cultivar versus non-cultivar population sources. *Restoration Ecology* 19:43–52.
- McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. “How local is local?” A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440.
- Meissen, J. C., S. M. Galatowitsch, and M. W. Cornett. 2015. Risks of overharvesting seed from native tallgrass prairies. *Restoration Ecology* 23:882–891.
- Vander Mijnsbrugge, K., A. Bischoff, and B. Smith. 2010. A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11:300–311.
- Miller, S. A., A. Bartow, M. Gisler, K. Ward, A. S. Young, and T. N. Kaye. 2011. Can an Ecoregion Serve as a Seed Transfer Zone? Evidence from a Common Garden Study with Five Native Species. *Restoration Ecology* 19:268–276.
- Moncada, K. M., N. J. Ehlke, G. J. Muehlbauer, C. C. Sheaffer, D. L. Wyse, and L. R. DeHaan. 2007. Genetic variation in three native plant species across the State of Minnesota. *Crop Science* 47:2379–2389.
- Mutegi, E., A. L. Stottlemeyer, A. A. Snow, and P. M. Sweeney. 2014. Genetic structure of remnant populations and cultivars of switchgrass (*Panicum virgatum*) in the context of prairie conservation and restoration. *Restoration Ecology* 22:223–231.
- Ploegstra, J. T., B. D. E. Ruyter, and T. Jelsma. 2015. Population genetic structure of *Asclepias tuberosa* in Northwest Iowa: A comparison within and between remnant prairies and commercially available seed. *Journal of the Iowa Academy of Science* 122:1–6.
- Selbo, S. M., and A. A. Snow. 2005. Flowering phenology and genetic similarity among local and recently introduced populations of *Andropogon gerardii* in Ohio. *Restoration Ecology* 13:441–447.
- Wagenius, S., H. H. Hangelbroek, C. E. Ridley, and R. G. Shaw. 2010. Biparental inbreeding and interremnant mating in a perennial prairie plant: Fitness consequences for progeny in their first eight years. *Evolution* 64:761–771.
- Wilsey, B. J. 2010. Productivity and subordinate species response to dominant grass species and seed source during restoration. *Restoration Ecology* 18:628–637.
- Wilson, L. R., D. J. Gibson, S. G. Baer, and L. C. Johnson. 2016. Plant community response to regional sources of dominant grasses in grasslands restored across a longitudinal gradient. *Ecosphere* 7:1–16.