Native Seed and Plant Sourcing

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Ecological restoration practices based on unproven assumptions or narrowly focused goals need to be re-examined. The overarching goal of a healthy ecosystem needs to be at the forefront of all decision making to ensure our big picture focus is not undermined or overly influenced by traditional practices that are not substantiated by objective science. One traditional practice needing re-examination is the use of geographic distance to define "local" seed sources. Because plants are strongly allied to climate the use of distance may not be the best option. In this paper, various seed sourcing concerns are defined and illustrated with examples before addressing problems arising from dependence on local genotype. Our once united landscape is now highly fragmented. Seeds from a region with similar climate and environmental variables can be successfully used to restore a site that will be resilient and capable of supporting a diverse biota. "Matching the Habitat" is the solution. Tools for understanding how to apply this concept include a seed sourcing table and maps.

The overarching goal of a healthy ecosystem needs to be at the forefront of decision making. Our big picture focus cannot be undermined or overly influenced by traditional practices that are not substantiated by objective science. We should not assume local seed sources, those defined by distance, will provide the desired outcome. This practice is more backward looking than forward looking as it does not address habitat fragmentation or climate change (Breed et al. 2013). In other words, the goal is to restore biologically diverse traits that allow for adaptation and the ability to bounce back from stresses. In doing this, we must understand the issues surrounding seed sourcing.

Plant population genetics are generally not random; they are structured by ecological factors such as climate, soil, and pollinators. Local-genotype seeds, sometimes referred to as local-ecotype seeds, have naturally evolved and adapted to a certain environment (Havens 2015). The genetic makeup inherited from the parent plants is the genotype. A plant's genetic makeup coupled with its adaptation to certain biotic and abiotic conditions is known as an ecotype. We tend to use the terms "local genotype" and "local ecotype" interchangeably but they are different. Local genotype refers to seeds or plants found nearby the restorations site while local ecotype refers to sources that are similar in climate and closely matches the restoration site.

Using local genotype seed is believed to be an imperative to restoration work as it assumes a plant's ability to flourish in certain environments. When this tenet is combined with a goal to restore a habitat to presettlement conditions, it also assumes to preserve the plant genetics of a particular area. Yet, there are many unanswered questions.

Local adaptation is assumed with plant populations near to the restoration site. Local is sometimes defined as within a few miles, others define it as within the same remnant. Gustafson et al. (2002) conducted the first study to quantify a distance; they found seed within 50 miles retains the local genotype. More recently, a survey of restoration practitioners in the Chicago area found they source their seeds 24-199 miles from the site they are restoring (Havens 2015). These examples – a survey and an empirical study - illustrate the notion that local genotype is defined by miles. Sourcing seed based solely on distance doesn't guarantee a healthy, resilient population. Jones (2013) found remnants and plantings with ecosystems "exhibiting complex biotic interactions" even though the plants were not "historically proximal;" this demonstrates plants do not have to co-evolve to "display desirable community-level interactions."

In lieu of the distance tenet, we need to evaluate the environments of the originating seed source and compare it with the environment of the seed destination (Havens 2015, Jones 2013, Pickup 2012, McKay et al. 2005, Bower et al. 2014). None of us wants to spend time and money on seeds that will not germinate or survive.

Seed Sourcing Concerns

It is important to understand six seed sourcing concerns and their negative effects. Below is a listing of each and a definition. Details and examples follow.

- Gene flow is the transfer of genes from one population to another (Lesica and Allendorf 1999).
- Gene swamping (aka gene pollution) is the overwhelming of local genes by introduced genes leading to the replacement of the local genotype (Vander Mihnsbrugge et al. 2010, Hufford and Mazer 2003).
- Inbreeding depression is reduced fitness (the ability to reproduce and contribute to the gene pool) from crosses within a related population (Vander Mihnsbrugge et al. 2010). It homogenizes the population genotype (Loveless and Hamrick 1984).
- Outbreeding depression is a result of lower fitness from crosses of different populations. This can lead to extinction if adaptation is impeded (Vander Mihnsbrugge et al. 2010; Krauss and He 2006).
- Founder effects are a type of genetic bottleneck caused by a loss of genetic variation when small populations are established from a limited number of sources (Hufford and Mazer 2003).
- Genetic bottlenecks are caused by a sharp reduction in the genetic variation of individual plants because of environmental catastrophes or anthropogenic activities, including collection procedures (Hufford and Mazer 2003).

Gene Flow and Swamping

Gene flow transfers genetic material by seeds and pollen with a more significant effect resulting from pollen transfer than from seeds. Gene flow is highly variable among species, populations, and individual plants and it can occur at considerable distances (Ellstrand 1992, Ellstrand and Elam 1993). Because many of our pollinators can fly several miles, a remnant located a few miles from a planted prairie is experiencing genetic mixing.

Gene flow can result in plants of the same genus hybridizing (Ellstrand 2002; Kramer and Havens 2009). This genetic mixing can have negative results, such as a plant displaying invasive tendencies, a plant with reduced vigor, (Hufford and Mazer 2003) a plant that is sterile, or extinction. Ellstrand (2002) found *Phlox pilosa* hybridized with *Phlox glabberima*, both native plants to Wisconsin. The result was a 15% drop in seed set because it was less attractive to pollinators.

Gene swamping occurs when non-local species overpower the local genes resulting in a loss of the local genotype. When *Lupine polyphyllus*, a western U.S. native, crosses with *Lupine perennis*, an eastern US native, the result is a genetic loss of *L. perennis* because *L. polyphyllus* takes on an invasive quality in the eastern region. Gene swamping isn't widespread (Lesica and Allendorf 1999; Jones 2013a; Krauss and He 2006); the risks are not well known (Helzer 2010, 162); and studies are rare (Sexton et al. 2014).

Outbreeding and Inbreeding

Outbreeding can reduce the health of a population when plant populations are mixed whereas inbreeding occurs with mixing within populations. How do we combat inbreeding without creating outbreeding?

Outbreeding depression is poorly understood (Vander Mihnsbrugge et al. 2010) and difficult to predict (Montalvo et al. (1997). It's impossible to discern between inbreeding and outbreeding depression without knowing the patterns of gene flow (Ellstrand 1992) and like outbreeding, it's also difficult to predict. Substantial decreases in fruiting and seed production can be indicative (Ellstrand and Elam 1993). The dangers of inbreeding outweigh the dangers of outbreeding (Edmands 2007).

Appropriately planted and managed seed orchards is another method for reducing the probability of inbreeding. Genetic diversity can occur with as few as 20 unrelated parent plants (Johnson et al. 2010) making this a feasible solution for an organization or a hobbyist.

Founder effects and Genetic Bottlenecks

Founder effects can occur when a population is established from a subset of the original population resulting in a loss of genetic diversity. Founder effects are immediate and can be exacerbated by a genetic bottleneck. Below is a simple depiction of how founder effects work and how the coupling of this with a bottleneck event compounds the loss of genetic diversity.

Ernst Mayr coined the term "founder effect" to distinguish this event from genetic drift (Barrett and Kohn 1991). Genetic drift is a random event; it affects a population's genetic makeup but not via natural selection. Using the depiction above, the bottlenecking event would be a random act such as a tree falling on certain plants in the prairie. Another example would be taking a small amount of seed from a large bag of seed and giving them to a friend. It isn't natural selection and it isn't a natural disaster but the resulting genetic drift is the same – lower diversity.

Genetic bottlenecks occur when a plant population is substantially reduced for at least one generation. The effect of a genetic bottleneck can take many years before it is noticed and can lead to extinction. An illustrative example of this is woolly milkweed (*Asclepias lanuginosa*) populations in Wisconsin. Before 1950 data from the Natural Heritage Institute (NHI) database show over 100 plants prior to 1980, decreasing to 10-50 between 1980 and 1990. While the database shows 0 in 2000, we know there are some populations remaining today (e-mail message from Corey Raimond, January 16, 2016). While we don't know the reasons for the sharp decline of woolly milkweed, it illustrates what one would expect to find in the data should a bottlenecking event occur.

Problems with Dependence on Local Genotype

Preserving the historic genotype and ensuring successful seed germination and plant establishment have been primary reasons for using local genotype. Yet, we don't have the necessary information to substantiate if we are successfully fulfilling this goal. We have no genetic information on most species or what level of genetic diversity needs to be maintained to ensure the plants thrive (McKay et al. 2005, Barrett and Kohn 1991, Johnson et al. 2010, Waller et al. 2011). Local adaptation is defined as a population that thrives in its original location, yet this concept is much less significant than once thought

(Bischoff et al. (2010). Most seeds are generally adapted, meaning they are well-suited to more than one environment (Jones 2013).

It's not always possible to locate a local seed source. The Driftless Area has many small roadside remnants, but these are becoming more difficult to find because of mowing or road construction. The encroachment of invasive plants is another factor reducing local seed populations. Genotypes adapted to survive and thrive in these new invaded ecosystems may not be those found locally (Jones 2013, Johnson et al. 2010). These changes and others "can significantly and possibly irreversibly change the local restoration environment beyond the limits where previously adapted species and communities can thrive" (Johnson et al. 2010). The solution is using genetically appropriate seeds and plants.

Logistic and economic feasibility of exclusively using local genotype seeds needs to be considered. We may not be able to locate sufficient amounts of seed to supply our restoration needs and rare and uncommon species may be extirpated. Realistically, we would not know if seed from our small remnants were genetically diverse without testing yet using seed that is not genetically diverse can thwart your goals for a healthy, resilient habitat (Bischoff et al. 2010). There are solutions, keep reading.

Other Factors to be Considered

Climate Change

Climate change will affect seed adaptability. The fragmentation of our landscape coupled with the changing climate will result in the inability of *in situ* genetic adaptation or migration of all organisms. Many species may not be able to adapt fast enough to survive. Long-lived perennials are currently "being forced to adapt or migrate" (Breed et al. 2013). Climate change is significantly influencing the risk of remaining rigid to the "local is best" paradigm. We need to reexamine our goals of trying to replicate a presettlement period by using only seed from nearby remnants. This practice can put restorations at risk of degradation and jeopardize the ecosystems we strive to save (Jones 2013, Harris et al. 2006, Breed et al. 2013).

Restorations need to be responsive to climate change. The genetic memory created by local adaptation will become less relevant as the climate changes (Jones 2013). We need to include a diverse range of species and genotypes (Heller 2009, Saari et al. 2012). For 20 years, scientists have been writing about the need for adaptation plans, yet how many of us understand what this really means? (Heller, 2009)

Disturbance Level of the Site

The disturbance level of the restoration site needs to be considered when sourcing seed. Using seeds from relatively undisturbed remnants to restore highly stressed land might not be adaptive. Rather than relying simply on geographic locale of the seed source, emphasis should be on genetically-adapted seeds and plants because they provide the highest fitness and adaptability (Johnson et al. 2010; Jones 2013).

Depending on the plant species, "high levels of genetic variation may be needed for long term persistence in severely disturbed sites" (Lesica and Allendorf 1999). Yet when the disturbance is minimal local seed might be more appropriate (Lesica and Allendorf 1999, Jones 2013). The goal is to establish healthy, resilient ecosystems. "Populations of multiple ecotypes are likely to show increased long-term stability compared to single-line populations" (Lesica and Allendorf 1999).

In 2013, Martin Breed and others proposed four types of seed sourcing options designed to "maximize establishment by acknowledging that evolution and environmental change are ongoing and can occur rapidly." Havens et al. (2015) created a table defining each of these four seed sourcing types; they also provide the benefits and risks of each and when these strategies would be best used.

Table 1. Types of seed sourcing, modified from Breed et al. (2013), with their description, benefits, risks and most appropriate uses.

Seed sourcing type	Definition	Benefits	Risks	Best Used When
Strict local provenancing	Using seed only from the site where restoration is occurring or populations within normal gene flow distance	• little risk of maladaptation (at least short term)	• narrow genetic base • possible inbreeding • genetic drift • lack of adaptive potential	• disturbance is minimal • large local population present at or adjacent to restoration • predicted distribution change is low
Relaxed local provenancing	Mixing seed from geographically close populations with a focus on matching environment of source and recipient sites	• little risk of maladaptation (at least short term) • avoids inbreeding • increases adaptive potential	• can have narrow genetic base • lack of adaptive potential for the longer term	• disturbance is minimal • predicted distribution change is low
Composite provenancing	Mixing seed from populations of close and intermediate distance (or environmental match) to mimic long distance gene flow	• avoids inbreeding • increases adaptive potential	• maladaptation • outbreeding depression	• disturbance is minimal • fragmentation is high • predicted distribution change is moderate
Admixture provenancing	Mixing seed from many populations of varying distances throughout the range of the species	• highest adaptive potential	• largest risk of maladaptation • outbreeding depression • possibly invasive genotypes	• disturbance is high • predicted distribution change is high
Predictive provenancing	Using genotypes adapted to predicted conditions (e.g. 2050 climate projections) based on models and transplant experiments	• deals best with changing conditions, if predictions are correct	• projections may be wrong • requires much research (high initial cost)	• disturbance is low to moderate • predicted distribution change is high and well understood

Havens, Kayri. 2015. Seed sourcing for restoration in an era of climate change. Natural Areas Journal 35(1): 122-133.

<u>The Solution: Matching the Habitat</u>

"Matching the Habitat" can be a viable option – economically feasible, logistically feasible, and genetically diverse. This is not a new concept as it was first recognized as a viable option in 1922 (Clausen et al. 1941). "Matching the Habitat" is based on finding similar environments to that of the restoration. Sometimes this can be a proximal location; other times it will be many miles away.

Two hundred years ago our habitats were contiguous; today they are fragmented. Coupled with the guidelines shown in the previous table, the following three maps are useful guides for seed and plant sourcing decisions. "Matching the Habitat" is easy. Identify your region from the Ecoregion map (Omernik and Griffith 2014; McMahon et al. 2001) or Plant Adaptation Region map (AKA seed transfer maps) (Vogel et al. 2005), then cross reference it with the USDA Cold Hardiness Zone map (USDA 2012) and you've matched your habitat! These three maps are included after the references. "Matching the Habitat" is economically and logistically feasible. When restorations span many acres, paying workers to seek out and collect the necessary amount of seed can be unaffordable. This also assumes local sources can provide sufficient quantities of the desired species. Often seed sourcing companies need to be used; many will commission seeds from within the ecoregion determined from "Matching the Habitat."

"Matching the Habitat" increases diversity and mixing non-local, generally-adapted seeds with local populations can have higher fitness (Vander Mihnsbrugge et al. 2010). The landscape of today is not the same as it was historically and climate change will create further divergence. Resilience must be a goal of our management activities; our restorations need to be able to survive climate change, fragmentation, and invasions of non-native plants.

Vander Mihnsbrugge et al. (2010) found that matching habitats of the seed to the habitat of the restoration is more important than a geographical delineation (Pickup 2012, Jones 2013a, Johnson et al. 2010, Wilkinson 2001, Hamilton 2001, Smith et al. 2010). Some disagree with this (McKay et al. 2005) but in a literature review, Jones (2013a) finds "documented cases of genetic mismatch are acknowledged as being scarce." As early as 1973 using seed from "multiple ecotypes" was endorsed as having a more stabilizing effect than seed from single sources (Lesica and Allendorf 1999).

Guidelines exist if you collect your own seed. Since most of our seed sourcing concerns result from low genetic diversity, to combat this, a strategic mixing of seeds from various plant populations can increase resilience (Jones 2013, McKay et al. 2005). Again, make sure your collection efforts are within your ecoregion and collect from a number of plant populations. Use the following guidelines to estimate genetic diversity in plant populations:

1. Species within small geographic boundaries have less genetic diversity than the same species found regionally (Ellstrand and Elam 1993, Loveless and Hamrick 1984).
2. Plant populations that increase via clonal growth are genetically more homogenized (Fant et al. 2013, Fant et al 2007).
3. Plants toward the edges of a population tend to have lower genetic diversity (Jones 2013).
4. Widespread species have more genetic diversity than those found in limited places (Ellstrand and Elam 1993).

Keeping meticulous and accurate seed source records is imperative and could assist future research. The capability to ascertain precise data about the adaptability of seed sources in a restoration could be greatly enhanced by our documentation skills. If we, as citizen scientists, maintain detailed seed sourcing records (i.e. PLS (Pure Live Seed) label from purchased seed, GPS of populations, number of plants in a population, etc.), the data would be available to an interested researcher. The outcome of this research could lead to a more thorough understanding of the dynamics of genotypes in restoration efforts.

Classic restoration practices will become more outdated and obsolete as our climate changes and ecosystems change with it. While this does not suggest we toss out the "local is best" paradigm; it does emphasize our need to be open to other options. There are times when "Matching the Habitat" is the better option. However one makes this decision, Kramer and Havens (2009) say it best: "Restoration efforts that disregard the importance of establishing and maintaining genetic as well as species diversity so do at their own peril."

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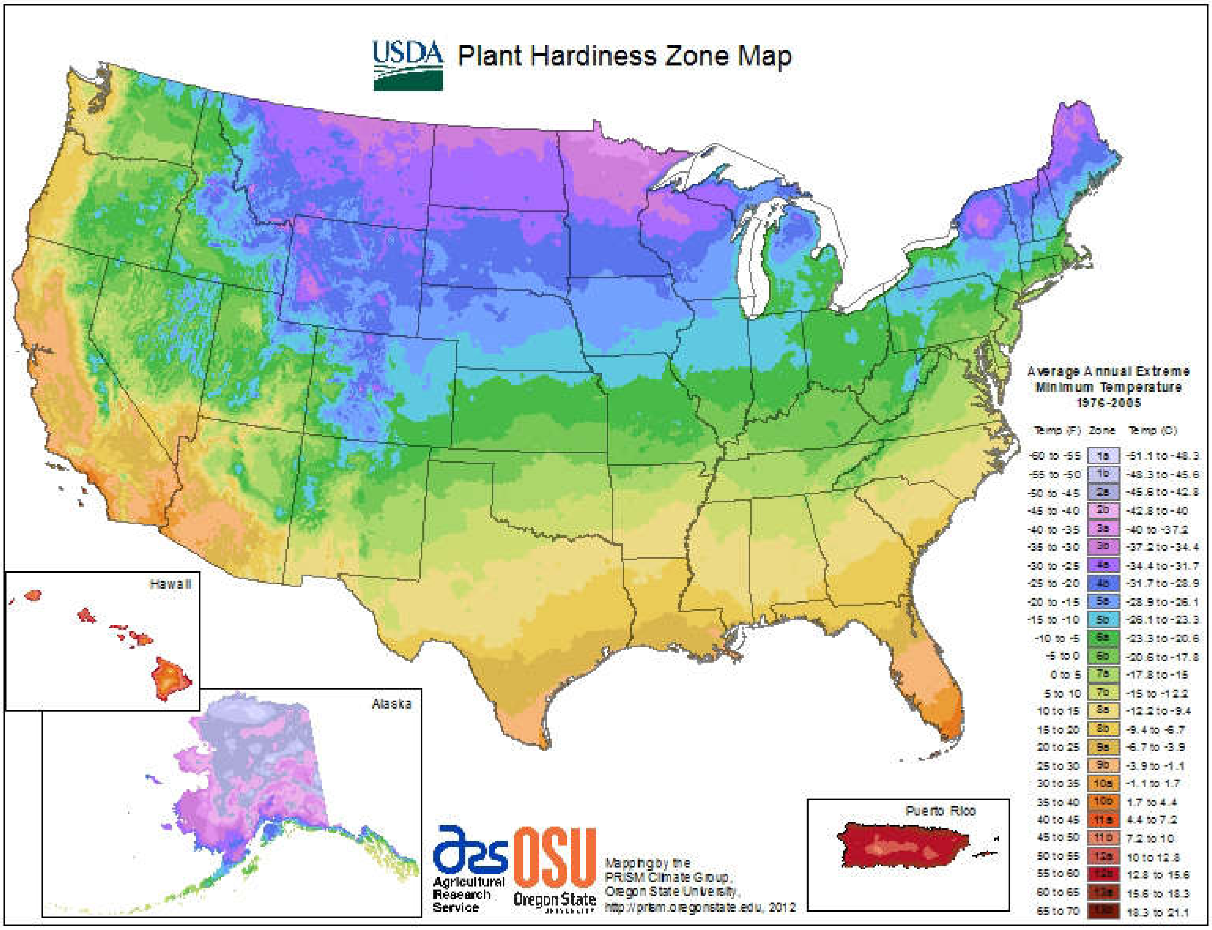
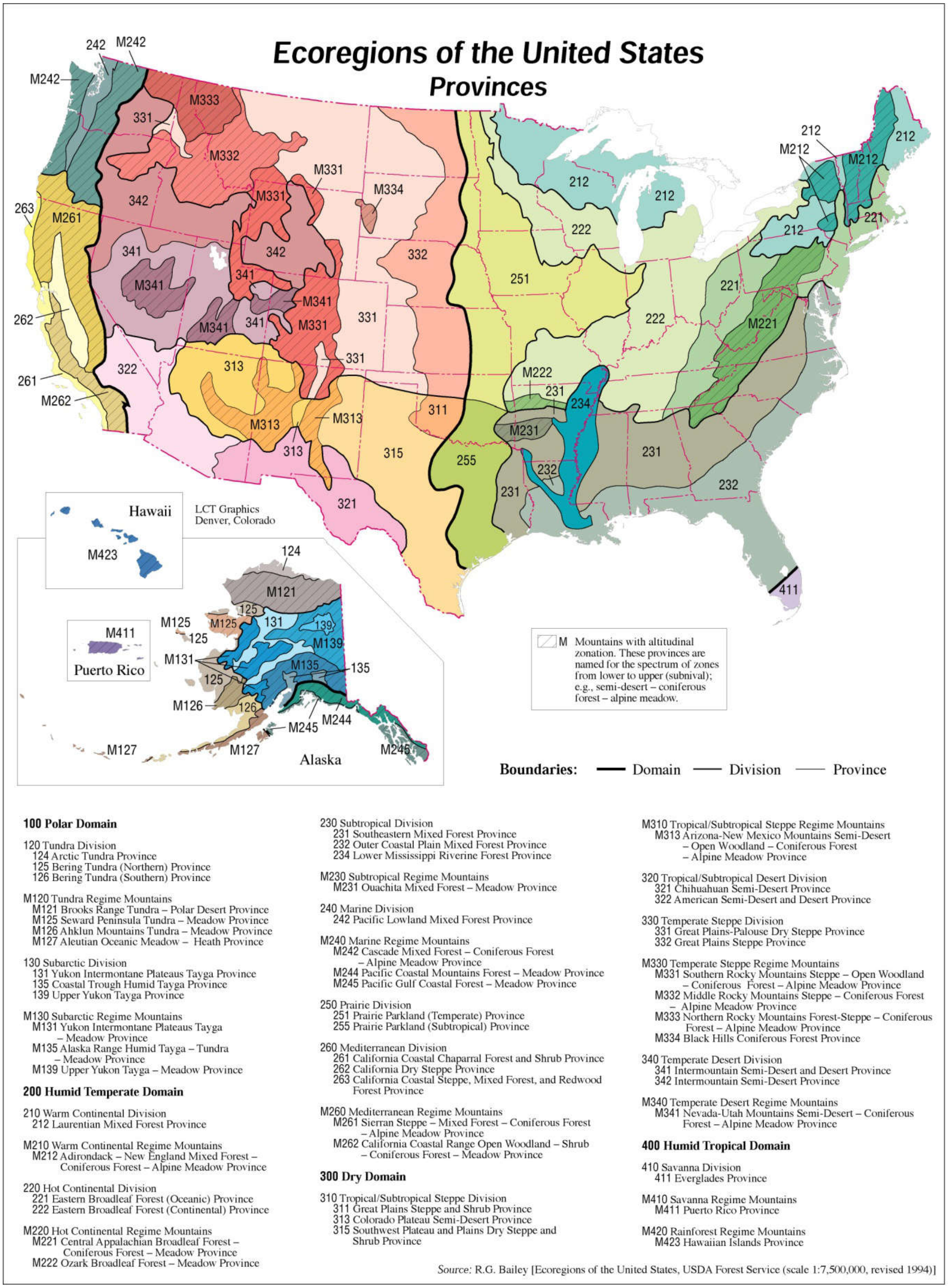
Maps

USDA Cold Hardiness Zones (USDA 2012)



Ecoregion map (Omernik and Griffith 2014; McMahon et al. 2001)



March 29, 1994

Plant Adaptation Region Map (AKA seed transfer maps) (Vogel et al. 2005)

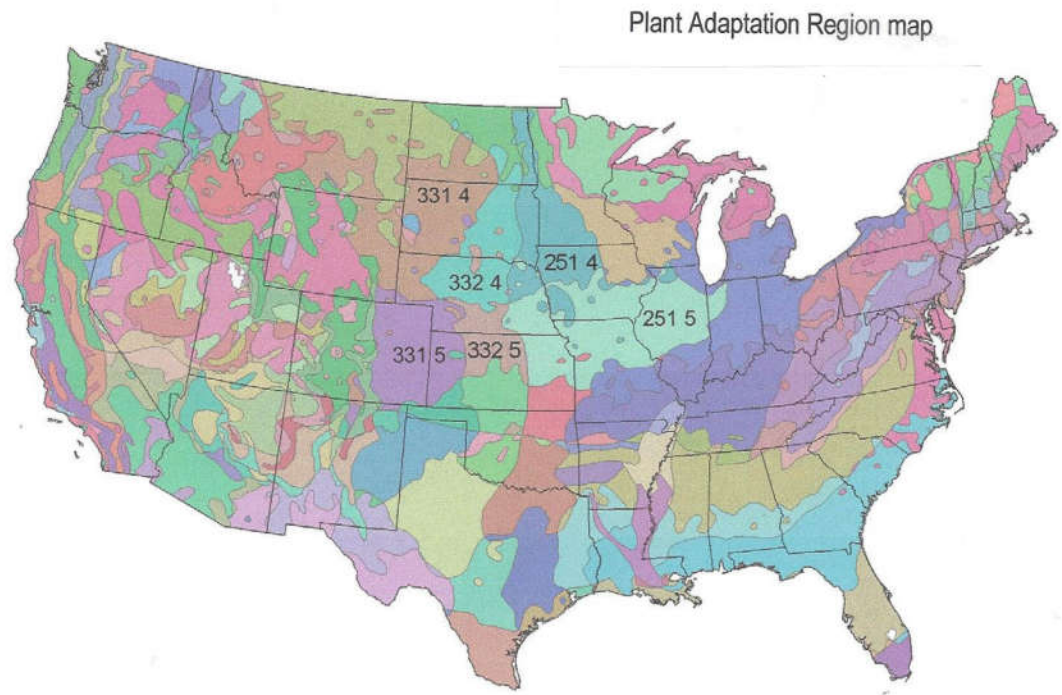


Figure 3. Plant Adaptation Region map for the United States minus Alaska and Hawaii with the following labeled PARs: PAR 331–4, PAR 331–5 = Great Plains Palouse Dry Steppe HZ4 and HZ5, respectively; PAR 332–4, PAR 332–5 = Great Plains Steppe HZ 4 and HZ5, respectively; PAR 251–4, PAR 251–5 = Prairie Parkland Temperate HZ 4 and HZ5, respectively.

Source: Vogel, K.P., M.R. Schmer, and R.B. Mitchell. 2005. Plant adaptation regions: ecological and climatic classificaion of plant materials. Rangeland Ecology and Management 58: 315-319.