Propagation Strategies

Genetic Considerations for Grassland Restoration in Oregon's Willamette Valley

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Grassland restoration is a management issue, not simply science. Like all management issues, it is a compromise between the desirable and the possible. I learned this on my first restoration project. Yield from local seed collection was tiny compared to the need, so I turned to seed purchases. No commercially available seed was derived from our county, but I considered the sources as acceptable. Commercially available seed included cultivated seed, seed increased for a generation or two from wild sources, and seed collected from the wild — in order of increasing cost. When I calculated how much seed I wanted of each species, the cost was $3200 per acre, more than the entire budget for the ten-acre site. I compromised.

Principles of population genetics should be considered when planning a grassland restoration, but compromise is usually necessary. First, we use these principles to determine what species and seed sources are most desirable, often making those choices despite lack of knowledge about population genetics of individual species. Second, we may compromise to match our desires to real limits of funding, time, and seed availability. Third, we review the plan to assure that it will not harm local stands of native plants and local genetic diversity. Lastly, we finalize the plan, realizing that if we cannot implement an acceptable restoration plan, exotic grasses will grow on the site and competitively exclude native Willamette Valley species.

Conservation biologists and geneticists agree that the best seed sources are wild local populations growing in the same habitats as those found in the restoration site (e.g. Linhart 1993). However, they disagree on how close the sources should be to the restoration site, whether matching microhabitats of source and restoration site is important, and whether using a mix of local and distant sources may be better than using only local sources. Restoration ecologists are interested in the discussion because local wild-collected seed which is carefully matched to individual microhabitats is the most expensive and time-consuming to collect and handle. What is desirable? What is minimally acceptable?

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My answers apply to Oregon's Willamette Valley, where grasslands have been fragmented for only about 160 years. Different rules apply in areas like the Great Basin, where populations may have been isolated for hundreds of thousands of years. My answers are generalizations. When information on genetics of an individual species is available, vegetation managers can craft more precise guidelines.

In this paper, "ecoregion" is defined as a large area with more or less homogeneous climate and vegetation. The ecoregion discussed consists of Oregon's Willamette Valley plus adjacent hills and valleys and part of southwest Washington. "Local populations" grow within I0 or 25 miles of the restoration site.

1. Genetic Integrity, Genetic Purity, Genetic Contamination, and Genetic Pollution

These phrases include so many different genetic issues that they are vague. They sound good, though. Use them for influencing decisions, but not for planning. When planning a project, identify the real genetic issues and determine their relevance.

2. Outbreeding Depression

This term, while sounding technical, is almost as vague as those above. Offspring that are hybrids between distantly related populations may have poor vigor, reproduce little, or die. The cause may one of the issues discussed below.

3. Adaptation/ Maladaptation

Plants from a distant source in a different environment may be poorly adapted to the restoration site. If they are so poorly adapted that they die, money and time are wasted but there is no genetic problem. For example, Idaho Fescue *(Festuca idahoensis* Elmer) is sometimes planted in western Oregon under the mistaken belief that it is native here. In reality, all *F. idahoensis* seed originates east of the Cascades. The species cannot tolerate western Oregon's high fungus populations and seem to need winter dormancy. When planted here, Idaho Fescue dies within a year.

If poorly adapted plants survive to reproduce, their genes may spread among local populations. Natural selection will limit this problem. The severity of the problem depends on the relative size of the introduced and native populations. If the introduced population is relatively small, its genetic impact on surrounding populations will be minimal. However, if the native (local) populations are very small compared to the maladapted introduced populations, maladapted genes could swamp the native genotypes and native populations could be destroyed.

An example of large-scale introduction of maladapted genotypes involves Ponderosa Pine *(Pious ponderosa* Dougl.) occurred in northern Idaho after the massive fires of 1920. Seed was used without regard to origin and no record of the sources was kept. Some stands have grown badly or succumbed to insects or disease. Maladapted genes have shown up in the offspring of more vigorous stands nearby, as well. This Ponderosa Pine example provides an important cautionary tale, but it is unusual because the introduced populations are extremely large compared to the unburned remnant native populations.

Distance between source and restoration sites does not necessarily predict adaptation. For example, showy partridge peas [*Chamaecrista fasciculata* (Muchx.) Greene] grew equally well whether they originated from local populations or from sources up to I000 km away, though plants from 2000 km away grew somewhat worse (Galloway and Fenster 2000).

4. Microhabitat Adaptation/ Maladaptation

The genome of a wild plant has been described as "not a fixed homogeneous entity but a deeply fissured, rapidly changing assembly of shapes" (Linhart 1993). Numerous studies have found short-range differences in plant morphology, isozyme profiles, or DNA (review in Linhart 1993). Some of these differences are genetic and clearly adaptive. Extreme differences in adaptation characterize plants living on potentially toxic soils like mine tailings rich in heavy metals, but differences can be found among plants growing on north-facing or south-facing slopes or growing high or low on the slope. Even the relatively uniform environment of Oregon's Willamette Valley presents plants with differences in soil texture, soil chemistry, water availability, temperature, and exposure to light and wind. Local populations often differ genetically and may (or may not) be finely adapted to these small-scale differences.

Individual or population-based variation is not necessarily microhabitat adaptation. It may result from phenotypic plasticity. For example, at Mary's Peak the *Festuca roemeri* growing on rock outcrops has short grayish blue leaves and is more similar to plants of serpentine soils in southwest Oregon than to the tall, blue-green plants of nearby meadows. When they are transplanted to a uniform environment, the differences disappear. If two populations grow in uniform but different environments, this sort of phenotypic plasticity can be mistaken for genetic differentiation among populations. A common garden study, where plants from different sources are grown together, can distinguish the two. Even if genetic differentiation occurs, it may not be adaptive. In *F* roemeri, the difference between hairy and glabrous leaves is genetic. Hairy leaves are very rare in the Willamette Valley. Do the hairy-leaved plants found south of Eugene constitute a distinct ecotype? Possibly, but not probably; glabrous plants inhabit similar habitats. Non-adaptive genetic variation is especially common self-pollinating species such as *Elymus glaucus.* In that species, ecotypes do exist (Snyder 1950) and some isozyme variation is related to habitat (Wilson et al. 2000). However, genetic differentiation has been observed at distances as short as 200 m in apparently uniform habitats (Knapp and Rice 1996), and much of the variation not associated with environment or genetic distance among populations (Knapp and Rice 1996, Wilson et al. 2000).

Although differentiation among local population may result from phenotypic plasticity or individual genetic variation, some is truly adaptive. What is the restoration biologist to do about small-scale adaptive differentiation? One recommendation is to use extremely local seed sources, within 100 m for herbaceous plants and within I km for trees (Linhart 1993). Another is to match source and restoration site habitats carefully. These approaches may be impractical if seed sources meeting these criteria are not available, if money and time are limiting, or if the restoration site includes several microhabitats.

A careful look at differentiation in populations of wild plants suggests an alternative approach. For example, *Veronica peregrina* growing in California's vernal pools are differentiated. Plants growing in the water, near the water's edge, and in nearby grassy areas differ genetically in both isozymes and physiology (Keeler 1978, Linhart 1974, Linhart 1976, Linhart 1988). Restoring a vernal pool thus seems to require collecting and planting V *peregrina* seed in concentric rings around the pool. However, seed dispersal and movement of pollinating insects among the rings must prevent these rings from forming isolated gene pools, suggesting that seed could be mixed and sown throughout a restored pool. This hypothesis is supported because the species survives in a pool that was plowed yearly, stirring the seed bank.

Other studies have found similar patterns at larger scales. The isozymes (genetic markers) associated with plants growing low on a slope occurred on similar microhabitats over large areas in plants as different as Wild Oats *(Avena barbata* Brot.) of California (Hamrick and Allard 1972) and Ponderosa Pine of Colorado (Mitton et al. 1977). This phenomenon provides evidence for microhabitat adaptation, but it also provides evidence for gene flow. The most likely explanation for this pattern is that pollen or seed spread genes more or less uniformly over a large area and then selection imposed the observed microhabitat differentiation. The process can be rapid; Wild Oats has been in California for about 500 years.

If gene flow normally crosses microhabitat boundaries, the restoration ecologist can mimic natural processes by mixing seed from many microhabitats. Using seeds from a variety of locations and microhabitats may insure that at least some of the seeds will grow in each microhabitat in the restoration site (Lesica and Alllendorf 1999). Eventually natural selection will impose a pattern on local population genetics even though seeds were originally planted uniformly

The Meadow Checkermallow *(Sidalcea campestris* Greene) is unusual because plants have different leaf shapes, depending on whether it lives on the east or west side of the Willamette Valley. Obviously genes are not flowing between these two groups of populations. We do not know if this difference is due to chance or related to some adaptation but it is genetic. It seems best to avoid mixing the two forms, at least until more is known about the species.

Before leaving the topic of adaptation, I must comment on misuse of the term "ecotype." We expect outbreeding depression from hybrids between different ecotypes because ecotypes differ genetically in adaptations to different environments. In the native plant business, word "ecotype" is often misapplied to populations that do not differ genetically in traits useful for adaptation. If the restoration ecologist collects bluish, glabrous Roemer's Fescue *[Festuca roemeri* (Pavlick) E. B. Alexeev) from the edge of a grassy bald in Douglas-fir forest in the Coburg Hills east of Eugene, bluish, hairy Roemer's Fescue from oak savannah on a hill top south of Eugene, and green, glabrous Roemer's Fescue from oak savannah low on a slope in Corvallis, has she collected three different ecotypes? Probably not. The differences may be phenotypic, and if they are genetic they may not be markers for different adaptations. (In this example, the differences are genetic, but hybrid vigor, rather than outbreeding depression, characterizes the hybrids; personal observation.) When the restoration ecologist collects from different populations, she has different accessions (collections), which may or may not be different ecotypes. Don't use "ecotype" for "accession."

5. Competitive Exclusion

It is theoretically possible for introduced populations of native plants to *he* better adapted to local environmental conditions than local plants of the same species. If so, the introduced lineage will replace local genotypes. Competitive exclusion by non-local native plants is not a serious problem. If microhabitat adaptations are important, local plants should be better adapted than any introduction. Even if species is a habitat generalist, introduced native plants are unlikely to be better adapted than local populations.

The probability of competitive exclusion varies depending on sources and breeding systems. Cultivated strains are the least likely to out-compete conspecific local populations because plants that have been in cultivation for generations tend to become adapted to cultivated fields, not natural ecosystem. Competitive exclusion by a non-local native plant is more likely to occur in self-pollinating or apomictic plants than in outcrossers. In selfers, beneficial mutation A which occurs in one lineage may never meet beneficial mutation B which occurs in another lineage. Therefore, a superior lineage with both mutations A and B is unlikely to form. If such a lineage is introduced, it may be highly competitive. In outcrossing plants, the few beneficial genes from superior plants will spread and mix with local genes, but wholesale extinction of local genotypes will not occur. This might be termed genetic contamination, although it is difficult to consider it a problem.

The competitive exclusion of practical concern for grassland managers occurs when exotic introduced species like Tall Fescue *(Festuca arundinaceous* Schreb.), Colonial Bentgrass *(Agrostis capillaris* L.), and shrubs replace native species. Use of exotics for erosion control, weed suppression, pasture renovation, and other restoration purposes causes competitive exclusion to an extent that use of non-local natives never will.

6. Breaking up Co-adapted Gene Complexes

A co-adapted gene complex is a set of alleles which work together to solve a particular environmental challenge. Let's say that in population #1, the alleles that work well together are AA BB CC DD. In population #2, the corresponding alleles are as bb cc dd. If we bring plants from the two populations together, they may produce descendents with various combinations of genes, such as AA bb CC dd, or Aa Bb Cc dd. The combinations (complexes) that did work have been broken up, and the new combinations don't work well. Eventually natural selection will eliminate the descendants with unworkable allele combinations and probably the rarer of the two parental types. In the short term, this can be a problem if the introduced population is large relative to the native one and therefore a high percentage of the progeny have inviable or competitively inferior genotypes.

Breaking up co-adapted gene complexes is unlikely to be an issue for grassland restoration in the Willamette Valley because evolution of different, incompatible co-adapted gene complexes requires time and genetic isolation. Fragmentation of Willamette Valley grasslands began with white settlement 160 years ago. In the absence of relevant information about the species involved, it is more realistic to assume that Willamette Valley grassland species lack incompatible co-adapted gene complexes.

Note that plants isolated since the glaciers retreated 15,000 years ago, like the two Oregon populations of the sedge *Carex macrohaeta,* may have had time to form different, incompatible co-adapted gene complexes. Species isolated for millions of years on the mountain ranges of the Great Basin have certainly had time (though they may not have incompatible complexes). The potential importance of this genetic issue depends on local history.

7. Loss of Genetic Diversity

Most wild populations are genetically diverse. Within the overall genetic uniformity of a species, each local population may have its own allele frequencies, rare alleles, or linkage groups. These characteristics can be preserved and, to some extent, spread if each revegetation project uses only local seed sources.

Wherever possible, multiple sources should be used. This helps preserve genetic diversity because many remaining populations of native grassland species are small, disturbed, and vulnerable to extirpation. Using many of these remnant stands as seed sources in each revegetation project creates "back-up" populations that are reserves for these genes. It also permits creation of new gene combinations, perhaps replacing combinations that have been lost.

Using many of the small populations in a restoration project also permits creation of new gene combinations, perhaps replacing combinations that have been lost. No one population of a rare plant contains all the genes that were present in the species before white settlement. Each population has, at most, the genes its ancestors did when the population became isolated (founder effect). Each small, isolated population may have lost genes by chance (genetic drift). Grassland remnants are often in extreme habitats unsuitable for cultivation — rock outcrops, steep slopes, wetlands, and soils with unusual proportions of elements where selection pressures may cause loss of genes for adaptation to mesic sites. However, many of our restoration sites have mesic environments. Recovering the best combination of genes for survival on mesic sites may require plants from many different grassland remnants.

Often local seed sources cannot provide enough wild seed for a project. Therefore, seed mmay be increased in cultivation. To minimize loss of genetic diversity and maintain necessary adaptations, seed increase should be done for few generations. Cultivation should be done in an area near the restoration site and in similar habitat.

Although seed increase for a few cultivated generations is an accepted practice for virtually all restoration projects, use of selected cultivars of native plant species is more controversial. It is possible for cultivars to become so adapted to cultivated fields that they are unable to survive in the wild, although this is rare with the native species of interest for restoration because are breeders usually select for good initial establishment in the wild. Selected cultivars are much less variable that wild populations. Therefore, using one cultivated source over a wide area does not directly help preserve local genetic diversity, although it is unlikely to harm local genetic diversity as long as local populations are undisturbed. Use of cultivated natives may aid preservation of genetic diversity indirectly by reducing competitive exclusion by introduced exotic species.

Cultivated seed has advantages. It is usually far less expensive than wild-collected seed and is more reliably available in large quantity. The decision to use it must be made in light of the projects goals and resources. If preserving local diversity is a goal, local seed sources should be used, perhaps supplemented with locally cultivated plants. If stopping soil erosion is the goal, a cultivar is perfectly acceptable, provided it originated in the ecoregion and is sufficiently well adapted to the restoration site habitat to grow there.

Vegetation managers occasionally want to know if a given rare species retains enough genetic variation to cope with environmental change. This question assumes that biologists can assess how much variation the species will need in the future, and that if the plant does not meet some standard of genetic diversity, it is unsalvageable. More genetic variation is better than less, but certain plants thrive with very little. Rarity itself is not a reliable predictor of genetic variation (Gitzendanner and Soltis 2000), but aquatic and wetland plants, long-isolated small populations, recently evolved rare plants, and high polyploids are often invariant or nearly so. Low genetic variation may cause inbreeding depression in a plant that recently lost variation, but low genetic variation in itself is not a predictor of population decline or extinction.

8. Inbreeding Depression

In the concern about genetic integrity and genetic contamination, the issue of inbreeding depression is likely to be ignored. Inbreeding is a decrease in vigor, survival, or reproduction in offspring of closely related parents. It may result from the pairing of rare, recessive, harmful alleles or from a general loss of heterozygosity.

The importance of inbreeding depression is probably underestimated for Willamette Valley grassland species. Populations below fifty are often considered safe from inbreeding depression, but grassland populations may be lower than that. For example, one remnant population of Roemer's Fescue consists of thirteen individuals (pers. obs.) Also, the degree of inbreeding depends on the effective population size. The effective population size is lower than the number of individuals present, and reflects the number of individuals that fail to set seed, individual differences in seed yield, and yearly fluctuations in reproductive success.

Harmful effects of inbreeding may be subtle. It may go unnoticed except for hybrid vigor in plants produced in crosses. For example, wild-collected Roemer 's Fescue produces healthy plants in cultivation, but the F I hybrids among different Willamette Valley populations are larger, more vigorous plants with many more seed heads (pers. obs.)

Inbreeding depression is most likely to be a problem for outcrossing native plants that were common and widespread until recently. It is irrelevant to self-pollinating or asexual plants. It is no longer an issue for very small populations that have survived as tiny isolated populations for thousands of years; they have lost their harmful alleles.

Inbreeding depression is not likely to result from the restoration process itself. If the species becomes established at the restoration site, its population will increase quickly and few alleles will be lost. If several well-chosen seed sources were used, the restored populations will experience hybrid vigor rather than inbreeding depression. Although hybrid vigor is greatest in the first hybrid generation, it declines slowly and will be a characteristic of the restored population for many generations.

9. Historic Patterns of Gene Flow

Gene flow is the movement of alleles (genes) within and among populations. In plants it occurs mainly through the dispersal of seeds and pollen. Asexual propagation though bulbils, rhizomes, and other fragments is important in some species. Gene flow is important for restoration ecologists for two reasons. First, one of the goals of habitat restoration is, or should be, reestablishing historical patterns of gene flow or compensating for their loss. Second, historical patterns of gene flow delineate the boundaries for seed transfer zones.

Brushy *fence* lines, strips of riparian forest, and greenways function as wildlife corridors, allow raccoons, deer, and other wild animals to travel between populations. No such corridors are available for grassland plants in the Willamette Valley. Roadsides could perform this function, but they are normally planted to exotic species (Tall Fescue, Colonial Bentgrass, etc.) and these species competitively exclude native species. Restoration sites may never fully connect natural grassland remnants, but their restored plant communities can compensate for the loss of gene flow by mixing alleles from different populations.

Although we cannot measure presettlement gene flow, we can make some rough estimates of its extent by observing the forces that spread seeds, pollen, and other propagules through the Willamette Valley and adjacent areas now. Most seeds and pollen grains move short distances but a few move much further. Rare but regular gene movement can knit plant populations together across a wide area, creating one extended gene pool or metapopulation.

Primary seed dispersal is movement of the seed from the mother plant to its first resting place in the soil. Fruit adaptations for primary seed dispersal include hooks that stick seeds to fur or clothing, parachutes for traveling by wind, brightly colored berries that are eaten and cause birds to deposit seeds in their feces, and corky layers that cause seeds to float. Wind-dispersed seeds can cover long distances, floating seeds can move downstream for miles, and animals dispersed seeds may travel as far as their host moves in the day or so it takes the seed to leave the animals. However, many grassland plants have no special adaptation for long-distance seed dispersal. Their primary seed dispersal consists of a fall from the parent plant to a spot a few inches or feet away. Such plants depend heavily on secondary seed dispersal. Secondary seed dispersal is movement from the place where the seed lands to the place where it germinates. Secondary seed dispersal via automobiles and ships is extremely effective. Secondary seed dispersal was doubtless less extensive but still important in presettlement times.

The swollen Willamette River rafted trees, shrubs, tangles of roots, and no doubt seeds downstream during 1996. The great flood of 1861 was of similar magnitude but was not controlled by dams. It flooded the Willamette Valley from the base of the Coast Range foothills on the east to the base of the Coburg Ridge and other foothills on the west. It moved human artifacts from Eugene to Portland and beyond. That hundred-year flood must have moved seeds and other plant propagules mainly downstream but also from side to side in the river's great braided channel. Water's effectiveness at moving upland plants may be demonstrated by collections of *Carex mops,* an upland Cascade Range species, from terraces of the Willamette River near Salem, Oregon (herbarium specimens at the Willamette University Herbarium (WILLU). Extensive flooding is a rare but regular event, but every year rain, streams, and small floods contribute to seed dispersal.

In general, floods disperse seeds downstream, but some 17,000 to 15,000 years ago, floodwaters moved plant parts (along with icebergs, boulders, and silt) south (what is now upstream) in the Willamette Valley. These great Bretz floods were produced by the breakup of glacial dams as glaciers retreated from the Clark Fork of the Columbia River in Idaho. Although they occurred too long ago to affect current patterns of gene flow and genetic differentiation, they are important because they thoroughly mixed seeds from the lower elevations of the entire Willamette Valley ecoregion.

The importance of secondary seed dispersal in mud on humans and other animals has been discovered repeatedly for over a century, and as often ignored. Ungulates are particularly effective for this method of seed dispersal because mud and plant debris collects between their paired hooves. For example, for at least three generations the Wilson family killed all weedy Common Sunflowers *(Helianthus animus* L.) on the family farm in Iowa. Nonetheless, a few Common Sunflowers grew on the farm each year, up to half a mile from the nearest seed source. How did they get there? Their location was a clue; most grew up near deer trails. Dispersal by ungulates like *deer* and elk is particularly important to Willamette Valley grasslands because it may cover long distances uphill and across the divides between watersheds.

The role of Native Americans in plant dispersal has probably been underestimated. Native Americans managed Willamette Valley vegetation intensively by burning grasslands and oak savannas (Johannessen et al. 1970), weeding camas meadows, and controlling competition around preferred plants. Doubtless they dispersed some preferred species over long distances and across watershed boundaries. The sedge *Carex barbarae* may provide an example. Native Americans cultivated *C. barbarae* beds to encourage production of long, unbranched rhizomes and traded the processed rhizomes, which were prized for basketry. They probably transported live rhizomes across the Rogue/Umpqua divide to establish populations on the Umpqua River.

In addition, pre-settlement Native Americans must have dispersed seed unintentionally in all the ways familiar to modern botanists; accidental loss of desirable seed, contamination in bulk seed collections, seeds imbedded in baskets and clothing, seeds stuck in mud on clothes and skin, and little packets of miscellaneous seeds or bulbs transported by children. What is particularly important for our purposes is that Native Americans crossed ecosystem and watershed boundaries. Each year, some individuals traveled the length and width of the Willamette Valley for purposes of trade, ceremony, family meetings, and hunting. Seeds traveled with them.

Pollen dispersal is another form of gene flow. Neighborhood sizes calculated from measured pollen flow can be small; those for *Viola rostrata* are approximately 25 m^2 (Levin 1986). However, pollen may travel far enough to affect population genetics. Therefore, recommended isolation distances for research fields of crop plants vary from 300 m to 1.6 km, depending on the pollination mechanism (Briggs and Knowles 1967). On our Iowa farm hybridization occurred between planted Sudan Grass *[Sorghum bicolor* (L.) Moench)] and a population of weedy conspecific Shattercane three quarters of a mile away (pers. obs.).

In animal-pollinated plants, pollen movement depends on how far the animals travel. Most pollinating insects spread pollen only several yards. Hummingbirds can be vectors for long-distance pollen dispersal, especially for plants that flower during migration. Butterflies are not considered efficient pollinators because they often move between different species, but swallowtails, large sulfurs, and most brushfoots can be important agents of long distance pollen dispersal because of a mating system called hilltopping. The males all fly to the tops of nearby hills (feeding and pollinating on the way up) and fly about there, waiting for females. Females fly to the hilltops, mate, and fly back down to lay eggs (feeding and pollinating on the whole round trip). This behavior mixes genes between plants of the valley floor and surrounding hills.

Regular gene flow across half a mile, three quarters of a mile, or a mile makes us look beyond the boundaries of microhabitats and tiny prairie remnant to find seed sources, but it is small compared to the extent of the Willamette Valley. However, these movements were cumulative, spread in all directions, and were interspersed with rare, very long range dispersal.

Conclusions

Gene flow slowly knitted together the populations of grassland species. It tied together conspecific plants of the Willamette Valley, adjacent hills, larger adjacent valleys, and a bit of southwest Washington into one large gene pool. Therefore, sites in this entire ecoregion can be considered appropriate seed sources for habitat restoration throughout the region.

This Willamette Valley ecoregion does not include the coast, where plants are often adapted to strong wind and salt spray, nor does it include high elevation sites where plants are dormant in winter and bloom much later in summet than plants of the valley floor. Botanists dispute whether this ecoregion includes all grasslands between the Umpqua River and southern British Columbia. During the climate fluctuations that accompanied retreat of the glaciers, the flora moved around this entire area in complex patterns not entirely understood. For Willamette Valley grassland restorations, it is probably best to avoid seed sources south of the Calapooia Divide or north of southern Washington, except in special cases such as Golden Paintbrush *(Castelleja levisecta* Greenm.), extirpated from Oregon but surviving in northwest Washington

Using multiple seed sources is strongly recommended. This helps preserve genes from all the sources used, reverses possible inbreeding depression, compensates for loss of gene flow, and provides a type of insurance in case microhabitat adaptation will prevent seed from some populations from growing at the restoration site.

Choice of seed sources should be based in part on genetic principles. The importance of these genetic considerations varies with the breeding system and abundance of the species involved, with the history of the natural populations in the area, and the type of restoration project.

For self-pollinating and asexual plants (including those that set seed without fertilization), outbreeding depression, inbreeding depression, and the breakup of co-adapted gene complexes are irrelevant concerns. Populations are greatly differentiated genetically, but this is more likely to be due to individual and family differentiation than to microadaptation. Plants with mixed mating systems and outcrossing plants with very limited gene flow are likely to have genetically differentiated populations and are the most likely to be finely adapted to microhabitat differences. Common outcrossing plants with long-distance gene flow are vulnerable to inbreeding depression after populations become fragmented and reduced. They may have microhabitat adaptations that are maintained by selection, but are unlikely to have incompatible co-adapted gene complexes.

Great population differentiation, microhabitat adaptation, and sometimes incompatible co-adapted gene complexes are expected in plant populations that have been isolated for many thousands or even hundreds of thousands of years (like those on mountains of the Great Basin). These traits may also be found in plants isolated since the glaciers retreated some 15,000 years ago. They are unlikely in the Willamette Valley grassland plants that have been isolated for no more than the 160 years since white settlements.

The kind of restoration project done also influences the choice of seed sources. The more sensitive the project, the more important it is to use only local sources. Enhancing an existing native grassland calls for different standards than preventing erosion control on a roadside (Table 1).

Any grassland restoration project is a compromise between the desirable and the possible. It is important to know what is most desirable, but also to be able to choose the best practical alternative. Producing a successful, genetically acceptable restoration is difficult but worth the effort.

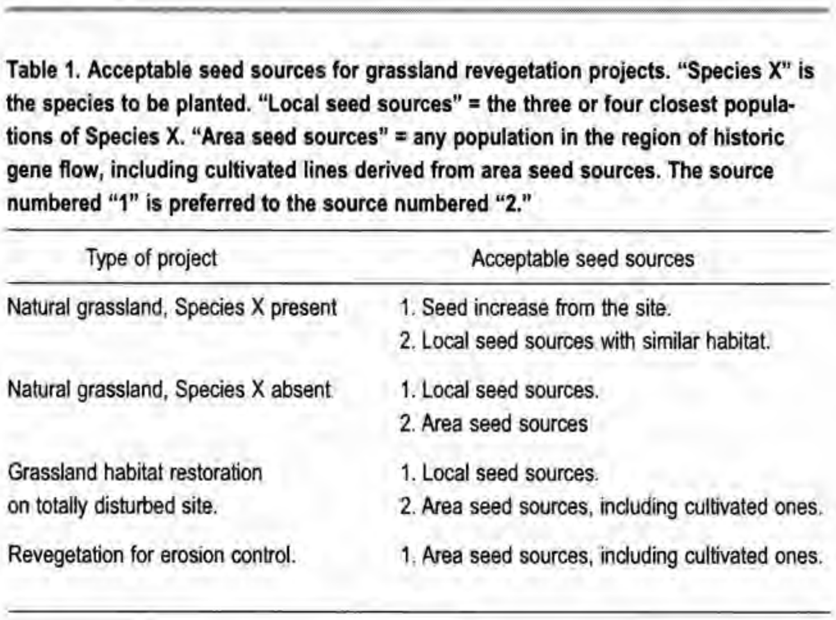

Table 1. Acceptable seed sources for grassland revegetation projects. "Species X" is the species to be planted. "Local seed sources" = the three or four closest populations of Species X. "Area seed sources" = any population in the region of historic gene flow, including cultivated lines derived from area seed sources. The source numbered "1" is preferred to the source numbered "2."

Type of project	Acceptable seed sources
Natural grassland, Species X present	1. Seed increase from the site. 2. Local seed sources with similar habitat.
Natural grassland, Species X absent	1. Local seed sources. 2. Area seed sources
Grassland habitat restoration on totally disturbed site.	1. Local seed sources. 2. Area seed sources, including cultivated ones.
Revegetation for erosion control.	1. Area seed sources, including cultivated ones.

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