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What are the best seed sources for ecosystem restoration on BLM and USFS lands?

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ABSTRACT

Native plant restoration policy calls for use of "genetically appropriate" native plant material on USDI Bureau of Land Management (BLM) and USDA Forest Service (USFS) lands. In this article, we summarize experimental evidence showing that local adaptation is widespread in all kingdoms of life, and how this "home-field advantage" has been exploited in forest restoration activities to develop and promote regionally adapted, genetically diverse restoration materials. The importance of regionally adapted, genetically diverse materials is highlighted in the context of changing environmental conditions, such as those predicted in future climate change scenarios. Although the adaptive properties of most restoration species remains unexamined, numerous tools exist for identifying similar environments and ecosystems, and these can be used to develop first-generation seed zones. Finally, general recommendations for establishing foundation populations are outlined so that pre-adapted populations retain sufficient genetic diversity to acclimate to new evolutionary challenges, while minimizing the likelihood of deleterious genetic outcomes (for example, inadvertent selection of undesirable traits; inbreeding depression).

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Federal land management agencies such as the USDA Forest Service (USFS) and USDI Bureau of Land Management (BLM) are required by law to manage their lands for multiple use objectives and to ensure long-term diversity and sustainability (Collins and Stritch 2008). Since the establishment of these agencies, a number of laws (summarized in Appendix 1) have been passed that govern public restoration activities on public lands totaling more than 182 million ha (450 million ac) nationwide, or nearly one-quarter of the land area of the US. These federal statutes dictate that public lands be managed to provide the American public with products and ecosystem services in a sustainable fashion. As a consequence, these agencies are directly and indirectly responsible for managing, conserving, and protecting genetic resources (species, ecotypes, populations, and genes) for a myriad of species, many of which play key roles in healthy ecosystems and sustainable landscapes.

An important facet of the sustainable land management mission is the restoration of ecosystems on lands that have been adversely affected by disturbance to the point that they no longer represent a state within the range of recorded historical variability (Lesica and Allendorf 1999; Jones and Monaco 2007; Jones and Monaco 2009). (Disturbances can include encroachment of nonnative invasive species, such as plants, animals, insects, and disease; unsustainable harvest of products; and changes in the frequency of fire and catastrophic wildfires.) In the past, restoration activities on federal lands attempted to restore ecosystems to an idealized, predisturbance state. Because ecosystems are not static, but instead respond to changing conditions through successional stages, *many* legitimate pre-disturbance states are represented within a historical range of variability, and therefore, many restoration goals are possible. When sites are severely degraded, restoration to one or more of these historical states may not be feasible. In such instances, realistic revegetation objectives could include either rehabilitation, recreating ecosystem function as best as possible with plant material characteristic of those in the past, or reclamation, creating an ecosystem that provides a subset of ecosystem services, with revegetation and soil stabilization being the driving goal (Lesica and Allendorf 1999; Jones and Monaco 2007). Similarly, climate change considerations must be addressed when planning restoration activities (Rice and Emery 2003; Jones and Monaco 2009).

Restoration on federal land is more than simply establishing a forest plantation or developing range areas for grazing. The primary purpose of federal ecological restoration is to implement land management actions that ultimately produce a "healthy" landscape or ecosystem (forest, savanna, grassland, and so on) that is capable of becoming self-sustaining, and one that provides for the diverse products and ecosystem services that society demands from public lands (Collins and Stritch 2008; Table 1). In the short term, restored ecosystems should provide immediate benefits in the form of soil stabilization, biotic diversification, and the necessary forage and food to support dependent flora and fauna. In the long term, restored ecosystems are expected to be sufficiently diverse and resilient that they can adapt to new and unpredictable environmental variables, such as climate change, invasive species, community/species redistribution, pathogens, and other biotic and abiotic challenges. The basic building blocks required to meet these short- and long-term needs are genetically appropriate native plant materials.

In the diverse ecosystems represented by USFS and BLM lands, natural genetic variation is typically structured across landscapes, with different populations exhibiting different characteristics that are the complex product of natural selection to climatic, biotic, and edaphic stresses, and random changes in gene frequency that are collectively referred to as genetic "drift" (for example, Clausen and Hiesey 1958; Knapp and Rice 1998; Johnson and others 2004). Many "native" restoration species have been developed to address the needs of landscape restoration practitioners; however, the historically narrow focus of selective cultivar development makes them less capable of developing these functionalities, or of recreating the kinds of structure that is characteristic of natural populations.

Because of the efficiencies inherent in agronomic development (Jones 2009), most releases of "native" or "restoration" species are limited in number and have more narrowly defined roles due to their selective and breeding history. These roles can include selection for rapid germination or establishment for soil conservation purposes; enhanced aboveground biomass accumulation for use as feed, fuel, or fiber; and enhanced seed production or evenness of ripening for even greater agronomic efficiency. Although agronomic releases are indeed "improved" relative to unselected founding populations, the purposes of these releases address narrower uses than are mandated by federal law. In combination, the limited number of available releases and the reduced genetic diversity makes it difficult, if not impossible, for federal agencies to recreate the kind of genetic structure and variation that mimics healthy native landscapes and ecosystems in restoration efforts. For these reasons, agronomic selections are genetically inappropriate for a subset of federal land management restoration/rehabilitation projects (for example, Lesica and Allendorf 1999), as they fail to address the myriad ecosystem services that federal lands are required by law to provide.

To conserve the range of genetic variation within species, which is the

TABLE 1

Ecosystem services classified by the Millennium Ecosystem Assessment *(2005).*

Supporting services
Wildlife habitat
Nutrient cycling
Soil formation
Primary production

Provisioning services
Food (crops, livestock, wild foods, and so on)
Fiber (timber, wood fuel, cotton, and so on)
Fresh water
Biochemicals, natural medicines, and so on
Pharmaceuticals

Regulating services
Air quality regulation
Climate regulation
Water regulation
Erosion regulation
Water purification and waste treatment
Disease regulation
Pest regulation
Pollination
Natural hazard regulation

foundation for adapting to the future environmental change and alternative restoration targets, genetic diversity, genetic structure, and future adaptability need to be included in our restoration programs. To achieve these management goals, restoration efforts on USFS and BLM lands are best served through the use of *locally adapted* and *regionally appropriate* native seed sources. Such seed sources will help ensure that the newly established plants are adapted to the current planting location and environment and will be favorably positioned for adapting to future climatic conditions.

ARE LOCALLY ADAPTED, REGIONALLY APPROPRIATE SOURCES ALWAYS BEST?

Many authors have discussed the genetic composition of seeds needed for native plant and landscape restoration (for example, Knapp and Rice 1994; Lesica and Allendorf 1999; Burton and Burton 2002; Rogers and Montalvo 2004; Jones 2005; McKay and others 2005; Jones and Monaco 2007; Broadhurst and others 2008; Jones and Monaco 2009; Kramer and Havens 2009). The majority opinion among these authors suggests that if site degradation has not been severe, "local" and "diverse" seed sources are a logical starting point.

The basis for this consensus comes from a wealth of reciprocal transplant studies, representing all kingdoms of life, that provide strong evidence of adaptation to local environments in resident populations (Table 2; also see Antonovics and Primack 1982; Xie and Ying 1995; Linhart and Grant 1996; Nagy and Rice 1997; Montalvo and Ellstrand 2000; McKay and others 2001; Wright and others 2006; O'Brien and Krauss 2008; Hereford 2009). Numerous common-garden and provenance studies have demonstrated inferior performance of seed sources that were collected too geographically distant from the planting site (for example, Wakely 1944; Squillace and Silen 1962; Hiesey and Nobs 1970; McGraw 1987; Xie and Ying 1993; Galloway and Fenster 2000; Annese and others 2006). Granted, these types of studies can fail to show local superiority (Schmidtling 2001; summarized in Hereford 2009), but most empirical studies identify local populations to be well-adapted to their home sites. Experience with conifer reforestation programs has also demonstrated that seed sources can perform poorly if moved too far from their geographic origin, and as a result, seed movement guidelines are dogma for forest tree species (Cunningham 1975; Rehfeldt 1987; Illingworth and Szalkai 1993; Randall 1996; Schmidtling 2001; Randall and Berrang 2002; Ying and Yanchuk 2006). In summary, the assumption that "local is best" is hardly a cliche or maxim. Such an assumption is a scientifically defensible starting point for restoring landscapes because natural selection applies different forces in different environments, and populations can respond by adapting to unique environments and locations (Hereford 2009).

If local adaptation is the norm for the plant kingdom, under what conditions might local sources *not* be the best for restoration? As noted by many authors (Lesica and Allendorf 1999; Rogers and Montalvo 2004; Jones 2005; McKay and others 2005; Jones and Monaco 2007; Broadhurst and others 2008; Jones and Monaco 2009), the most pressing cases for the use of non-locally adapted materials are those in which the target environment has been so substantially degraded or altered by natural or anthropogenic processes that it is outside the normal environmental "adaptive envelope" of resident populations or (in extreme cases) resident species. Dramatic and (or) sustained changes in soil properties (chemical, physical, biological), competition (from invasive species), pathogens and (or) herbivores (native and introduced), and fire regimes present significant challenges to restoration practitioners because they can significantly (and possibly irreversibly) change the local restoration environment beyond the limits where previously adapted species and communities can thrive. In these extreme cases, we agree with authors who conclude that local populations will be less than optimal (Lesica and Allendorf 1999; Jones 2005; Jones and Monaco 2007; Jones and Monaco 2009). Nevertheless, even in these cases the need for pre-adapted and genetically diverse planting materials does not go away, as the constantly changing suite of pathogens and potential eli-

TABLE 2

Evidence from reciprocal transplant studies showing local sources as optimal or near-optimal (Figure 4). Additional studies are summarized in Hereford (2009).

Family	Common name	Species (reference)
Trees		
Betulaceae	Red alder	*Alnus rubra* Bong. (Hamann and others 2000)
Cupressaceae	Atlantic white cedar	*Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb. (Mylecraine and others 2005)
Fagaceae	Red oak	*Quercus rubra* L. (Sork and others 1993)
Pinaceae	Grand fir	*Abies grandis* (Douglas ex D. Don) Lindl. (Xie and Ying 1993)
Pinaceae	Pines	*Pinus contorta* Douglas ex Louden (Ying and Hunt 1987; Ying and Liang 1994; Xie and Ying 1995; Wu and Ying 2004); *P. lambertiana* Dougl. (Harry and others 1983); *P. ponderosa* C. Lawson (Squillace and Silen 1962; Wright 2007); *P. taeda* L. (Wakely 1944; Frank 1951)
Shrubs/Forbs		
Apiaceae	Largeleaf pennywort	*Hydrocotyle bonariensis* Comm. ex Lam. (Knight and Miller 2004)
Asteraceae	Yarrow	*Achillea millefolium* L. (Hiesey and Nobs 1970)
Asteraceae	Sagebrush	*Artemisia tridentata* Nutt. (Wang and others 1997)
Asteraceae	Serpentine sunflower	*Helianthus exilis* A. Gray (Sambatti and Rice 2006)
Balsaminaceae	Jewelweed; Touch-me-not	*Impatiens capensis* Meerb. (Schmitt and Gamble 1990); *I. pallida* Nutt. (Bennington and McGraw 1995)
Caryophyllaceae	Oneflower stitchwort	*Arenaria uniflora* (Walter) Mattf. (Wyatt 1986)
Caryophyllaceae	Catchfly	*Silene ciliata* Pourret (Giménez-Benavides and others 2007)
Chenopodiaceae	Fourwing saltbush	*Atriplex canescens* (Pursh) Nutt. (Petersen and Ueckert 2005)
Chenopodiaceae	Glasswort	*Salicornia europaea* L. (Davy and Smith 1985)
Ericaceae	Labrador tea	*Ledum groenlandicum* Oeder (Riebesell 1981)
Fabaceae	Partridge pea	*Chamaecrista fasciculata* (Michx.) Greene (Galloway and Fenster 2000; Etterson 2004)
Fabaceae	Deerweed	*Lotus scoparius* (Nutt.) Ottley (Montalvo and Ellstrand 2000)
Fabaceae	Red clover	*Trifolium pratense* L. (Joshi and others 2001)
Onagraceae	Clarkia	*Clarkia xantiana* A. Gray (Geber and Eckhart 2005)
Plantaginaceae	Narrowleaf plantain	*Plantago lanceolata* L. (Joshi and others 2001)
Polemoniaceae	Bluehead gilia	*Gilia capitata* Sims (Nagy and Rice 1997)
Polemoniaceae	Sticky polemonium	*Polemonium viscosum* Nutt. (Galen and others 1991)
Ranunculaceae	Twolobe larkspur	*Delphinium nelsonii* Pritz. ex Walp. (Waser and Price 1985)
Rosaceae	Oneseed hawthorn	*Crataegus monogyna* Jacq. (Jones and others 2001)
Rosaceae	Mountain-avens	*Dryas octopetala* L. (McGraw 1987; see Annese and others 2006)
Rosaceae	Sticky cinquefoil	*Potentilla glandulosa* Lindl. (Clausen and others 1940)
Scrophulariaceae	Spinster's blue-eyed Mary	*Collinsia sparsiflora* Fisch. & C.A. Mey. (Wright and others 2006)
Scrophulariaceae	Purple monkeyflower	*Mimulus lewisii* Pursh (Angert and Schemske 2005)
Zosteraceae	Seawrack	*Zostera marina* L. (Hammerli and Reush 2002)

TABLE 2

Evidence from reciprocal transplant studies showing local sources as optimal or near-optimal (Figure 4). Additional studies are summarized in Hereford (2009).

Family	Common name	Species (reference)
Graminoids		
Poaceae	Colonial bentgrass	*Agrostis tenuis* L. (Bradshaw 1960)
Poaceae	Pineland three-awn	*Aristida stricta* Michx. (Kendell and others 1996)
Poaceae	Texas grama	*Bouteloua rigidiseta* (Steud.) Hitchc. (Miller and Fowler 1994)
Poaceae	Orchardgrass	*Dactylis glomerata* L. (Gauthier and others 1998; Joshi and others 2001; Annese and others 2006)
Poaceae	Barnyardgrass	*Echinochloa crus-galli* (L.) P. Beauv. (Potvin 1986)
Poaceae	Blue wildrye	*Elymus glaucus* Buckley (Rice and Knapp 2008)
Cyperaceae	Tussock cottongrass	*Eriophorum vaginatum* L. (Shaver and others 1986)
Poaceae	Common velvetgrass	*Holcus lanatus* L. (Bischoff and others 2006)
Poaceae	Foxtail barley	*Hordeum jubatum* L. (Wang and Redmann 1996)
Poaceae	Purple needlegrass	*Nassella pulchra* (Hitchc.) Barkworth (Rice and Knapp 2008)
Poaceae	Snowgrass	*Poa hiemata* Vickery (Byars and others 2007)
Mosses		
Polytrichaceae	Juniper polytrichum moss	*Polytrichum juniperinum* Hedw. (Hedderson and Longton 2008)
Soil microbial communities		Ayres and others 2009

mate change require diversity for future adaptability and ecosystem health.

HOW DO WE IDENTIFY LOCALLY ADAPTED, REGIONALLY APPROPRIATE GERMPLASM SOURCES?

Because preserving pre-adapted genotypes and the potential for future local adaptation is important in the restoration of public lands, a critical question is: How do we define "local"? Or, perhaps more practically: How far can we move a seed source and still have it be well-adapted to its new planting site? Local adaptation is a response to selective gradients in the environment; hence, theory suggests that the strongest cases of local adaptation will emerge from environments with steep selective gradients (Hereford 2009). Examples of steep gradients can include the change in temperature that occurs with elevation change in mountainous terrain, the changes in precipitation that occur in mountain rain shadows, the dramatic transitions in soil chemistry observed in serpentine versus non-serpentine soils, and changes in distributions due to biotic interactions (such as pathogens or competition). In this context, the question "How far?" is not necessarily a function of distance, but rather the rate of change in environmental gradients *over* distance, and the capacity of a species to adapt to change. For this reason, seed transfer guidelines based solelyon distance (for example, kilometers from source: Broadhurst and others 2008; Hereford 2009) are less likely to preserve adapted germplasm than those based on major selective gradients of environmental variables.

For the vast majority of species used in restoration, the information available on their landscape genetic variation and responses to selective gradients is insufficient to provide informed seed movement guidelines. In the absence of this information, reasonable climatic and landscape tools are available that can be used to minimize maladaptive responses to simple and complex selective gradients. For species and populations whose fitness is largely influenced by minimum temperatures, USDA Cold Hardiness Zones (Cathey 1990; Figure 1A), which are derived from average annual minimum temperatures, can be used to provide a simple transfer guide to protect plants from cold damage. Alternatively, ecosystems have also been formally defined through Ecoregion maps (Omernik 1987; McMahon and others 2001; Figure IB). These can be used as guides for identifying sites with common floristic and soil attributes, and can be used to provide broadly (Level III) or narrowly (Level IV) circumscribed seed transfer zones. Recently, Ecoregions have been merged with other climatic information to provide composite seed transfer maps.

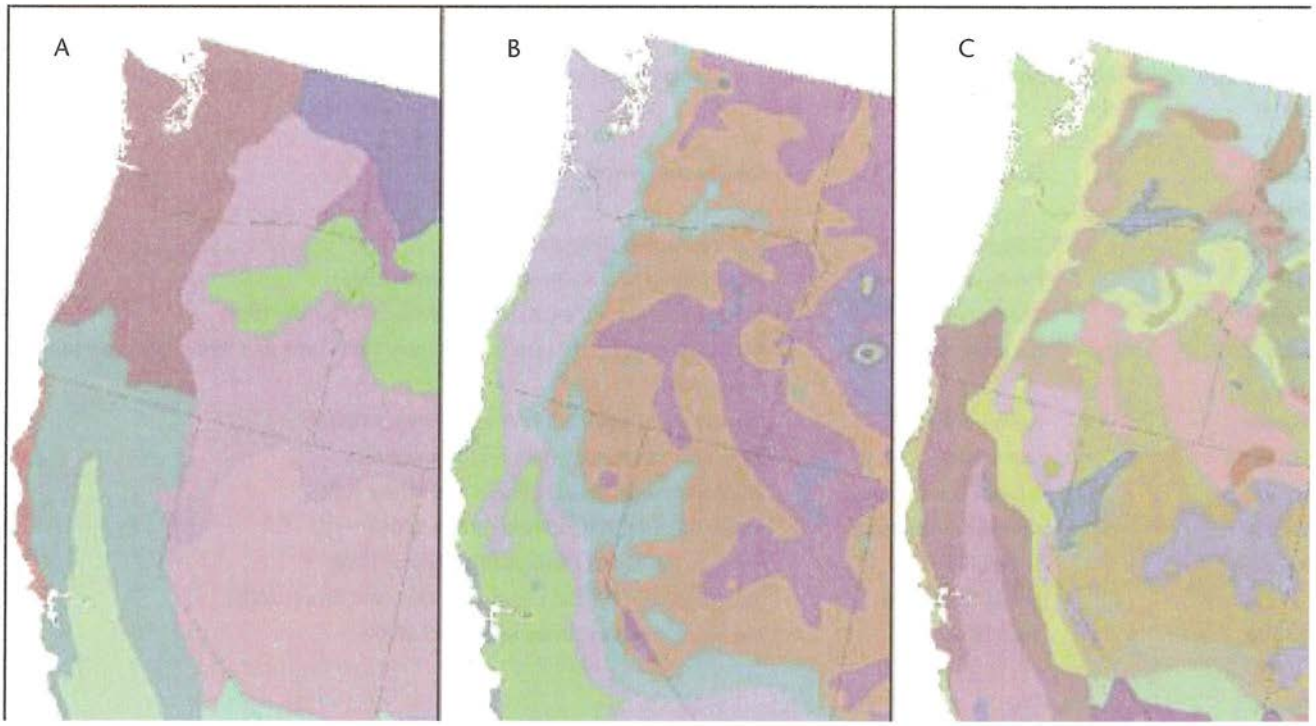

Figure 1. Alternative landscape classifications that can be used to guide seed zones in the Pacific Northwest. USDA cold hardiness zones (A); Omermik Level III Ecoregions (B); Plant Adaptation Regions (C), a product of the information contained in A and B.

For example, "plant adaptation regions" (Vogel and others 2005; Figure IC) merge Ecoregions and USDA Cold Hardiness Zones to account for local adaptation reflected in floristic associations and minimum temperature. In a similar manner, USFS geneticists have merged temperature and precipitation models to account for local adaptation that can be accounted for by these climatic factors (Bower 2010). Finally, more complex focal point models have been constructed that take into account biogeoclimatic (weather, aspect, soil, and edaphic) features of the landscape (Hargrove and Hoffman 2005). These latter models do not provide maps or predefined boundaries, but instead show the degree of similarity between source and potential planting sites in different dimensions of multivariate space.

For species previously evaluated in research settings, the answer to "how local is local?" is known to vary across regions and species. For example, based on common-garden studies, Rehfeldt (1994; Table 3) showed that conifer trees varied greatly in their patterns of genetic variation over the landscape; some are climatic generalists that can be moved into different climate "space" without a significant change in fitness, whereas others are climatic specialists that cannot be moved far out of their source environment without a decline in fitness. The degree of climatic specialization is intrinsic to species, as congeners showing nearly identical life histories and comparable ranges (for example, *Pinus contorta* Dougl. ex Louden and *P. monticola* Doug]. ex D. Don [Pinaceae l, Table 3) can show very different capacities for local adaptation. Common-garden studies of grasses show a similar range of climatic specialization. For example, *Poa hiemata* Vickery (Poaceae) (Byars and others 2007) and *Elymus gleucus* Buckley (Poaceae) (Erickson and others 2004) show local adaptation over small geographic and climatic scales (approximately equivalent to Omernik Level IV Ecoregions or smaller), while *Festuca roemeri* (Pavlick) Alexeev (Poaceae) shows less climatic specialization (seed zones approximate to Level III Ecoregions; Wilson and others 2008) and *Distichlis spicata* (L.) Greene (Poaceae) even less climatic specialization (seed zones approximate to Level III Ecoregions or larger; Rukavina and others 2008).

On USFS and BLM lands, a risk-adverse answer for "how local is local?" would be to use Level IV Ecoregions as a starting point for restoration materials. Ecoregions can be divided into finer zones or clustered in larger zones using climatic, community, soil, or related information to better represent the "steepness" of the observed selective gradients in landscapes and the phenotypic gradients displayed by resident populations. In the event that restoration species are evaluated in provenance or common-garden tests, provisional seed zones can be re-evaluated and modified to meet the available science.

TABLE 3

Conifer species and the amount of environmental difference needed to show a genetic difference (from Rehfeldt 1994).

Species	Elevation difference to find genetic difference m (ft)	Frost-free days to find genetic difference	Evolutionary mode
Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco [Pinaceae])	200 (656)	18	Specialist
Lodgepole pine (*Pinus contorta* Douglas ex Louden [Pinaceae])	220 (722)	20	Specialist
Engelmann spruce (*Picea engelmannii* Parry ex Engelm. [Pinaceae])	370 (1214)	33	Intermediate
Ponderosa pine (*Pinus ponderosa* C. Lawson [Pinaceae])	420 (1378)	38	Intermediate
Western larch (*Larix occidentalis* Nutt. [Pinaceae]) (Figure 5)	450 (1475)	40	Intermediate
Western redcedar (*Thuja plicata* Donn ex D. Don [Cupressaceae])	600 (1970)	54	Generalist
Western white pine (*Pinus monticola* Douglas ex D. Don [Pinaceae])	none	90	Generalist

WHAT KIND OF GENETIC VARIATION IS IMPORTANT TO RESTORATION?

Genetic variation is important, for without it, organisms cannot adapt to changing environments. For example, if a plant population lacks genetic variation in its ability to withstand heat and drought stress, its capacity for adapting to increasing temperatures will be hindered. The ability for a population to adapt is a function of the amount of genetic variation expressed and where the population is located relative to its adaptive optimum. At certain scales, the genetic structure and diversity of foundation species can be a key determinant of community-level traits and community diversity (Wimp and others 2005; Whitham and others 2006; Bangert and others 2008; Schweitzer and others 2008; Bailey and others 2009; Barbour and others 2009; Crutsinger and others 2009). For this reason, amount and kind of genetic diversity in the foundation species planted by the USFS and BLM can have a profound impact on short-term ecosystem services, and possibly the long-term diversity, adaptability, and health of a host of dependent species.

The value of genetic diversity in a restored population is dependent on the environmental context in which it is expressed. For this reason, the *magnitude* of diversity in a restoration source can be far less important than the *kind* of variation expressed. Adding new genetic variation to a population can be good, as long as it does not significantly increase the amount of maladapted genetic variation and result in a lower overall population fitness. In restoration, more genetic diversity is not always better (Rogers and Montalvo 2004).

Figure 2 shows an example of the trade-offs made in native plant restoration to balance the kind and amount of diversity required in restoration seed mixes. In this graph, the Y axis represents the relative proportion of individuals with their optimum fitness at some level of X, which represents an environmental gradient (for example, temperature, precipitation, or incidence of pathogens). The average fitness response for a species (Panel A, dashed line) is the product of *all* individual population-level responses, many of which may show different optima (or mean values for X), and which may also overlap for a specific value of X. In these hypothetical distributions, a genetically diverse population would show a wide fitness response (wide range of X values), whereas a less diverse

population (red arrow) would show a more uniform response (narrow range of X values).

In restoration activities, the ideal situation is to match restoration materials closely to an environment at or near their adaptive optimum. An example would be using seeds from population 8 (yellow line) to restore an environment that has an average value of 8 (Figure 2, panel B). In practice, this "ideal" situation is rarely realized due to the lack of knowledge concerning local adaptation and the limited availability of well-characterized seed sources. In practice, substituting genetically diverse seed sources from non-identical but similar environments (for example, substituting 6 [green] or 10 [black] for 8; Figure 2B) can still lead to restoration success because alternative populations can show substantial fitness overlap in the restored location. Substituting seeds from increasingly dissimilar environments (for example, seeds from population 4 [blue]; Figure 2B) increases the risk of a maladaptive response-even in genetically diverse materials-because smaller proportions of the restoration seed source will be pre-adapted to the restoration environment. This highlights an important point: adding large amounts of non-adapted genetic variation to a seed mix (as is practiced in the development of multiple origin polycrosses [Rogers and Montalvo 2004]) may not be desirable, because the proportion of pre-adapted seeds in the restoration mix could be a small fraction of the total input.

This simplified framework can be useful for considering the trade-offs and options that may be required to mitigate climate change. If a planting environment is expected to change in ways that are difficult to predict in the future (as might be the case with climate change), then the amount of genetic diversity present within restoration materials may be a critical factor for long-term restoration success. For example, if hypothetical conditions are expected to change in the near future from a value of 8 to 10 (Figure 2C), then the breadth of fitness responses in restoration materials may be more important than the average fitness value. In this example, the yellow and red populations have the same optimum, but the red population has one-fourth the genetic variance as the orange population. This is comparable to the reductions in genetic diversity of many highly selected (improved; bred) restoration cultivars. Because of its higher level of genetic diversity, the yellow population will likely be better suited for future adaptation than the red population, because yellow has a higher proportion of individuals pre-adapted to environment 10. Note that if the direction of change is known, it is possible to design populations that are better suited for both the current and future climates for a given level of genetic variation.

HOW MUCH GENETIC VARIATION IS NEEDED?

If more genetic variation is better (given that average fitness does not change), how much genetic variation is enough to maintain a population's adaptability? The answer depends on the time-frame considered and the objectives of the planting. Annual crops represent one end of the agronomic spectrum, as the narrow genetic diversity present in inbred lines, elite crosses, or single clones can be exploited by matching specifically adapted genotypes to a specific environment whose stochasticity is greatly ameliorated, resulting in maximum yield in a single growing season. Landscape restoration represents the other end of this spectrum, as these populations are expected to remain viable and adaptable for decades or longer in a highly variable and stochastic environment, without the luxury of repeated annual planting and maintenance (which is neither financially nor ecologically sustainable and sometimes not even permitted).

Because restoration seed sources typically are not the only representatives of a species, such sources need only sufficient numbers and genetic variation to be able to adapt to new conditions, rather than to maintain all rare (low frequency) variation in a species. To maintain a species, suggested numbers of parents are usually in the hundreds (Franklin 1980) or thousands (Lande 1995; Lynch and others 1995; Franklin and Frankham 2006) in order to preserve low-frequency genetic variation. The number of parents needed to preserve *population-level* ability to respond to artificial (or natural) selection over 10 or more generations is far lower, and values for unrelated parents from an outcrossing species (like maize) are between 10 and 40 (Baker and Curnow 1969; Kang 1979). If one further considers that seed parents could be related, either through localized inbreeding or clonal reproduction, theory suggests that one would need more parents (approximately twice as many) to maintain genetic variation for the mid-term. Species that are predominately selfing, apomictic, or clonal will be less sensitive to the effects of inbreeding than are outcrossing individuals, but could require even large numbers since recombination (sexual reproduction) is not available to provide new genetic combinations after selective events.

Maintaining a relatively large parental population will also decrease the opportunity for inbreeding. Inbreeding, or recurrent mating among genetically related individuals, is frequently problematic for outcrossing plant species. Numerous studies show that a reduction in fitness (inbreeding depression) can occur if population sizes are sufficiently low that relatedness accumulates in the population (Charlesworth and Charlesworth 1987).

Based on the literature, seed sources for ecosystem restoration efforts should have a relatively broad genetic base with at least 50 unrelated parents unless one can carefully control the contributions of each of the parents as we do in

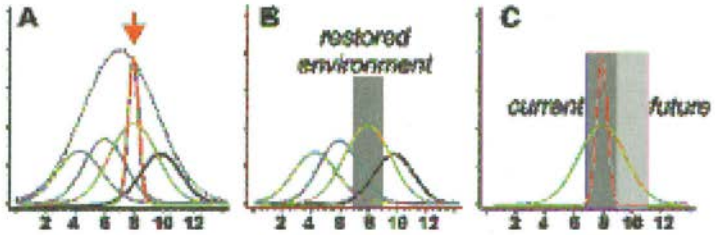

Figure 2. The average fitness response of a species (dashed line) is the product of many population responses, each with different levels of diversity and different optima for specific environmental factors (such as temperature; X-axis) (A). Diverse populations may have different optimal values for environment, but they can show substantial overlap if they are from similar environments (for example, population 8 shares overlap with population 6 and 10, but not population 4) (B). Genetically diverse populations (yellow) may be more capable of responding to changing environments than are highly selected populations (red), even if they show the same optima (C).

forest tree seed orchards. For seed orchard seeds, the USFS requires a minimum of 20 unrelated parents, a number that should provide the same level of risks as seeds collected from a natural population (Johnson and Lipow 2002). These numbers will be sufficient to allow populations to adapt to changes in the environment for many generations and to avoid inbreeding depression in the near future.

DO I WANT SEEDS SELECTED FOR A SPECIFIC TRAIT?

The promises of greater vigor, higher disease resistance, and greater seed yield offered by agronomically selected seed sources are attractive. At face value, it is easy to extrapolate from a vigorous seed increase field to a healthy sustainable ecosystem. In some cases, this gain may be realized, but agriculture offers striking examples of how selection for a few traits can bring unplanned, and occasionally disastrous, changes. One of the most noteworthy genetic "surprises" was the widespread selection for Texas (T) cytoplasm in maize breeding lines in the 1960s. This factor conferred male sterility, a feature that improved agronomic efficiency; it also conferred susceptibility to a previously uncharacterized race of the fungus *Cochliobolus heterostrophus.* The widespread incorporation of this germplasm into cultivars precipitated the southern corn leaf blight epidemic, an outbreak that destroyed 15% of the US maize crop in one year (Hooker 1974). This and similar examples provide cautionary warnings of the ecological risks associated with the widespread deployment of highly successful, highly selected agronomic releases.

Even under less intense selection regimes, unanticipated changes can occur in environmentally responsive traits. Growth rate for some species is often associated with temperature at the collection source (for example, St Clair and others 2005), so care must be exercised when selecting for vigor because indirectly selecting for reduced cold hardiness is possible. Adaptive diversity can even be unintentionally lost during the selection process when efforts are made to retain diverse collections *and* geographic genetic variation. For example, Level III Ecoregions were recently used as the basis for collecting germplasm for an oceanspray *(Holodiscus discolor* (Pursh) Maxim. [Rosaceae]) restoration seed orchard. Plants from 5 Pacific Northwest Ecoregion zones (Oregon: Cascade Mountains, Coast Range, Klamath Mountains, Willamette Valley; Washington: Puget Trough) were evaluated in a common garden (Corvallis, Oregon), and the most vigorous individuals were selected to develop Ecoregion-specific restoration releases. Re-analysis of the garden data revealed that Ecoregions accounted for far less of the variation among accessions than did winter temperature and precipitation (Horning and others 2008) (Figure 3). In fact, this study design led to the inclusion of genotypes that were *pre-adapted to the garden environment* (Willamette Valley), and these genotypes were outliers relative to plants from their source Ecoregion.

Among the continuum of seed materials available for restoration on federal lands, pre-varietal releases from the "source identified" and "selected" classes (also known as "primary" and "secondary" restoration gene pools [Jones and Monaco 2007)) have the highest potential for retaining a high level of adaptive diversity, especially when the number of founding parents is large. Older established cultivars (many of which are still in use after 50 y [Rogers and Montalvo 2004; Aubry and others 2005]), and cultivars derived from severe

Figure 3. Adaptive diversity of *Holodiscus discolor* Pursh Maxim. (Rosaceae) was unintentionally lost during the selection process for a seed orchard and actually led to inclusion of genotypes pre-adapted to the seed orchard environment. Photo bv Tara Luna

Figure 4. Reciprocal transplant studies with many species, including *Achillea millefolium* L. (Asteraceae), show that local sources are optimal or near-optimal for restoration plantings. Photo by Tara Luna

hybrid bottlenecks ("tertiary" restoration gene pools [Jones and Monaco 2007]), possess a very narrow and highly selected genetic base and are least suited to providing the diverse services required of public lands and landscapes. Because selecting on a mixed population for improved growth or seed yield can inadvertently alter or lower the overall fitness of a seed source at many of the potential planting sites, a logical way to select for specific traits is to make selections within one or multiple populations that are diverse and are appropriate for the seed zone in question. This framework is used for many agronomic and forestry breeding programs.

USFS AND BLM SEED NEEDS

The genetic resources needed for ecosystem restoration are different from those for annual crop agriculture or single-purpose environments. Germplasms used for ecosystem restoration need sufficient genetic variability to allow them to adapt over generations to a wide range of ever-changing biotic and abiotic factors, without regular augmentation through reseeding. These seed sources should begin with representatives that arise from an environment similar to that of the planting site; exactly how similar varies by species. Until research can quantify "how local is local?" for all restoration species, a reasonable seed source for restoration would be one from the same ecosystem, represented by more than 50 parents, and from at least 5 different locations (Withrow-Robinson and Johnson 2006). Sampling different populations within an ecosystem minimizes the opportunity for inbreeding and increases the opportunity that the winnowing effective of natural selection will leave some parents (and their descendents) well-adapted to the planting site. If environmental uncertainty is expected to increase in the future, as might be the case with climate change, these sampling strategies can be modified to include "composite provenances" (Broadhurst and others 2008) that include a wider array of genetic diversity that is adapted to a wider existing environment, or anticipated future environments.

Seed sources with narrow genetic bases that have been bred for agronomic traits may be appropriate for highly degraded lands (Lesica and Allendorf 1999; Jones and Monaco 2009), but for ecological restoration projects implemented on lands that are not severely disturbed, agronomic selections are generally not optimal. Given the paucity of desirable seed sources for ecosystem restoration, however, cultivars are often the only readily available seed that is deployable in a timely manner. With time, locally adapted, genetically diverse seed sources will become available on the market, and these will be the first choices of the BLM and USFS. Such types of seed releases are currently being developed by federal and private sources. Coordination of these efforts is underway through programs such as the Plant Conservation Alliance (http://www.nps.gov/ plants/), the Great Basin Native Plant Selection & Increase Project (http://www.fs.fed.us/rm/boise/

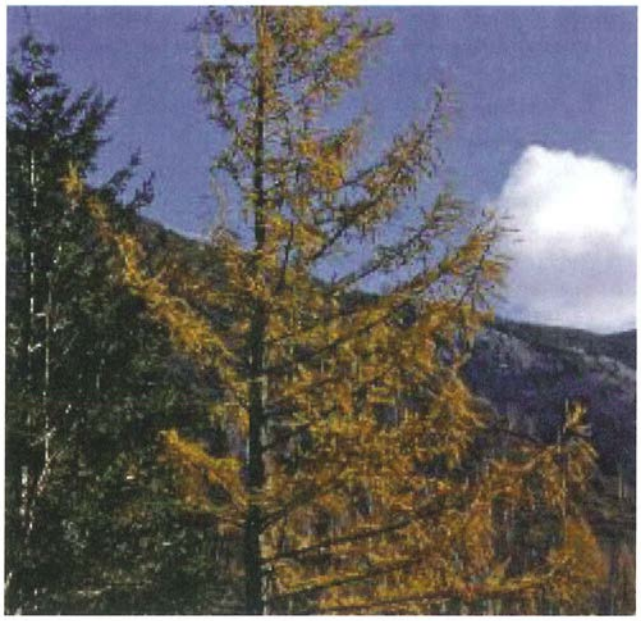

Figure 5. Western larch (*Larix occidentalis* Nutt. [Pinaceae]) can be moved 450 m (1475 ft) before genetic differences are noted. See Table 3. Photo by Tara Luna

research/shrub/greatbasin.shtml), and regional efforts such as the Willamette Valley Seed Increase Program (Ward and others 2008). Over the years, seeds used for restoration on federal lands have increasingly moved from nonnative to native species. In the future, we anticipate that most native restoration materials will derive from locally adapted, genetically diverse seed releases. To do this, both seed developers and seed producers will need to shift from cultivars to those sources desired by the BLM and USFS.

RECOMMENDATIONS

Based on the wealth of literature, seed sources for restoration of federal lands should be made up of parents that come from ecosystems ("seed zones") similar to those at the restoration site. This guideline improves the chances that the planted population will be pre-adapted to the restoration site. While local may not always be better than non-local sources, an extensive list of studies and literature indicate that non-local sources are far more likely to be maladapted to novel environments than are local sources.

Collecting seeds from parents from multiple locations within a seed zone or ecosystem to serve as foundation seeds increases the opportunity to broaden the genetic base of the restoration population. This broad base will provide the necessary genetic variation for natural selection to winnow poorly adapted genotypes and to select for pre-adapted genotypes. In those instances in which plants show a limited capacity to disperse, incorporating broader diversity into restoration gene pools may be important for providing opportunrties to respond to future environmental and evolutionary challenges. Diverse, locally adapted sources are also likely to show the lowest risk for future inbreeding depression (due to the mating between unrelated genotypes); similarly, the risk of outbreeding depression may be reduced since mating between resident and planted genotypes will primarily involve plants from similar seed zones and ecosystems.

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APPENDIX 1

Specific laws, regulations, and executive orders that support the use of native plants on federal lands.

1. Organic Administration Act of 1897 (16 U.s.c. §§473 *et seq.)*
2. Knutson-Vandenberg Act of june 9, 1930 (16 U.S.C. 576, 576a-576b)
3. Bankhead-jones Farm Tenant Act of 1937 (7 U.S.C. §§1010 *et seq.)*
4. Anderson-Mansfield Reforestation and Revegetation joint Resolution Act of Octoberl 1, 1949 (16 U.S.C. 581j [note], 581j, 581k)
5. Granger-Thye Act of 1950 (16 U.S.c. §§580h)
6. Sikes Act (Fish and Wildlife Conservation) of September 15, 1960 (16 U.s.c. 670g-6701, 6700)
7. Multiple-Use Sustained-Yield Act of 1960 (16 U.S.c. §§528 *et seq.)*
8. Wilderness Act of 1964 (16 U.s.c. §§1131 *et seq.)*
9. The Endangered Species Act (ESA) of 1973 (16 U.s.c. §§1531 *et seq.)*
10. Federal Land Policy and Management Act (FLPMA) of 1976 (43 U.S.c. §§ 1700 et. *seq.).* Section 102 directs management of public lands in a manner that will protect the quality of the ecological values; where appropriate, will preserve and protect in their natural condition; will provide food and habitat for fish and wildlife and domestic animals; and will provide for outdoor recreation and human occupancy and use.
11. Forest and Rangeland Renewable Resources Planning Act (RPA) of 1974 as amended by the National Forest Management Act (NFMA) of 1976, section 6 codified at 16 U.s.c. §§1600 (g)
12. Surface Mining Control and Reclamation Act of 1977 (30 U.s.c. 1201, 1201 [note], 1236, 1272, 1305)
13. Cooperative Forestry Assistance Act of 1978 (16 U.S.C. 2101 [note], 2101-2103, 2103a, 2103b, 2104-2105). Section 3 (16 U.s.c. 2102) details the assistance that may be given to state foresters or equivalent state officials and state extension directors, in the form of financial, technical, educational, and related assistance.
14. The North American Wetland Conservation Act 1989 (16 U.s.c. 4401 [note], 4401-4413, 16 U.S.C. 669b [note])
15. Section 323 of Public Law 108-7, the Consolidated Appropriations Resolution (16 U.s.c. 2104 [note])
16. Healthy Forests Restoration Act of 2003 (H.R. 1904), (16 U.S.C. 6501-6502, 6511-18, 6541-42,6571-78)
17. The National Historic Preservation Act of 1966 (16 U.s.c. §§470 *et seq.)*

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