Genetically Appropriate Choices for Plant Materials to Maintain Biological Diversity

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Foreword

Native plant material use in revegetation or restoration efforts has increased nationally over the past couple of decades, replacing to some extent our past reliance on European grasses. This shift to natives has raised questions about the selection of appropriate genetic stocks, similar to the issues involved in using native trees for reforestation. There is a need and an opportunity for dialog between land managers choosing native plant materials for wildland use, and geneticists who can provide counsel on relevant (but often complicated) details. This guide is intended to foster such a dialog. It synthesizes important genetic principles and provides many examples to better inform land managers, and help them understand the context for advice from geneticists. It focuses on details relevant to the USDA Forest Service's Rocky Mountain Region, but contains a wealth of information that is relevant elsewhere, as well.

Revegetation, restoration, or emergency rehabilitation efforts are conducted at the local level, but assistance can be provided from regional or national levels. Tools are needed to help local land managers make informed decisions when native materials suitable for the site are not commercially available (or feasible), and when seed transfer guidelines or seed zones have not been developed for the particular plant species of interest. Regional strategies can help provide guidance, and lead to economies of scale. Development of this Guide was the top priority in a strategic effort in the Rocky Mountain Region in 2002, to assist our National Forests and Grasslands in addressing their needs for native plant materials. The other products (for example, prioritized lists of species, seed procurement plans, native seed collections from the Forests and Grasslands, common garden studies) remain unfunded at this time.

A tremendous amount of scientific study, policy, and infrastructure support the use of merchantable native tree species for reforestation following timber harvest, fire, disease or insect epidemics, and other disturbances. But we are in the early stages of developing and incorporating genetic information into our selection of other native plant materials in public land management. There is also a significant need to understand the interplay between our choices of germplasm and its ecological interaction in the landscape (for example, competitive interactions, pollination ecology, herbivory, etc.). It is hoped that this Guide will be further developed over time or lead to the production of other documents, workshops, policies or procedures, and serve as a catalyst to elevate the need (increase the awareness) for native seed collections and common garden studies.

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Preface

This document was prepared as a guide to making genetically appropriate choices for native plant materials in revegetation projects. This being its most appropriate identity, ‘the Guide’ or ‘this Guide’ are used when referring to this document rather than the longer document title. In general, the flow of this Guide is from principles to specific decisions and case studies. The first several chapters provide information on why genetic diversity and integrity are important for native plant species and why they are worth conserving and considering in management decisions. Information is provided about the nature of genetic diversity, how it is shaped by natural processes such as selection and migration, and how we measure it. In Chapter 5, we place genetic diversity within the context of long-term evolutionary processes, ecology, and life-history characteristics of plant species. Through this review, we emphasize the relationships between genetics and ecology—important for two reasons. First, it underscores the consistency in natural features and processes: when we conserve genetic diversity and integrity, we are concomitantly conserving other ecological and ecosystem processes and values. Second, more often than not, sufficient and direct genetic information for a particular species is not available. Hence, understanding the relationships and correlations with life-history traits can help make an informed decision in the absence of direct genetic information. We consider these chapters to be important in strengthening the decision-making ability of Guide users, as well as providing the rationale and context for the guidelines we present later.

In Chapters 6 and 7, the information becomes more applied and focused on revegetation issues. Chapter 6 addresses the concepts of what are genetically local and genetically appropriate in the context of revegetation projects. In the following chapter the consequences of poor genetic decisions (or failure to consider genetic source) in selecting revegetation materials for a site are presented. At this point in the Guide, a foundation for making genetically appropriate decisions: explaining the genetic principles about the importance of maintaining genetic integrity, emphasizing the relationships between genetic diversity and ecological processes, and providing some sense of the risk involved when genetic decisions are not well made.

The information in chapters 8 through 11 directly address the decisions involved in genetic selections of plant revegetation materials. Chapter 8 covers the issue of what to consider when purchasing plant materials. Chapter 9 provides guidelines for how to make genetic decisions in a specific project. This chapter is no doubt an attractive, and hopefully useful, one for readers. But again, we emphasize that it is best used in the context of the information presented in other chapters. Chapter 10 is a resource of genetic information for some of the native plant species in Region 2 of the Forest Service, presented here as a convenient reference, but recognizing that new information is constantly available and Readers should not assume this chapter is comprehensive. Chapter 11 provides an opportunity for Readers to practice the guidelines presented in Chapter 9. We present here some real and theoretical examples and illustrate how the decision of what is genetically appropriate would be made, using our guidelines. A brief summary of the major messages in the Guide and some concluding comments are provided in Chapter 12. The Guide concludes with a glossary that contains some of the more technical words used in the chapters and boxes. The intent is to provide a brief definition that provides sufficient clarity for the reader to understand the term in the context in which it was provided in the text.

Some additional information is included as sidebars or boxes about topics that are mentioned in the text, for example, genetic policies of other organizations or agencies. This structure was chosen for additional information to allow Readers the opportunity to delve more deeply into some topics, without compromising the general flow of the main narrative.

We strongly recommend that Readers visit the introductory chapters before making use of the information in Chapters 8 through 11. The best use of our guidelines requires both an understanding of genetic principles which we have tried to effectively convey here, as well as the knowledge of site conditions and objectives and the valuable management experience that the reader possesses. Our objective is to better support with science the Readers' discretion, not replace it.

The PLANTS Database (http://plants.usda.gov/) of the USDA's Natural Resource Conservation Service has been used as the source of taxonomic information throughout the Guide.

Acknowledgements

This Guide was made possible by funding from the USDA Forest Service's Rocky Mountain Region and the University of California under a Joint Venture Agreement between the Forest Service and the Regents of the University of California (FS Agreement No. 03-JV-11020000-051; UC Proposal No. 03101065). It was designed to fill a gap seen by Andrew Kratz, Regional Botanist, Rocky Mountain Region. His interest in using the best available science in resource management, and in particular, making genetic information more accessible, was the impetus for creating this Guide. In addition to his initiative that led to the Guide's development, he has provided liberal amounts of materials to inform the Guide and has provided thoughtful reviews of earlier drafts.

Mary Frances Mahalovich, Regional Geneticist for the USDA Forest Service's Northern, Rocky Mountain, Southwestern, and Intermountain Regions, has been a strong source of support and wealth of genetic information in the preparation of this Guide. Her reviews of earlier drafts have assisted in keeping the utility of the Guide focused on the Forest Service mission, and in maintaining a strong scientific basis for the narrative.

Gay Austin provided considerable information and suggestions, reviewed an earlier draft of the Guide, and supported the development of this Guide with enthusiasm. Kat Anderson, Gay Austin, Richard Cronn, Norman Ellstrand, Vicky Erickson, James Hensen, Valerie Hipkins, Randy Johnson, Scott Peterson, Chuck Quimby, John Randall, Leslie Stewart, and Nancy Warren have reviewed and provided helpful comments on all or particular sections of this Guide. We are very grateful for their interest and their contributions.

Many other individuals—including Norm Ellstrand, Laura Galloway, Subray Hegde, Keli Kuykendall, E. Durant McArthur, Patrick McGuire, Steven Monsen, Leonard Nunney, Chris Richards, and Ken Vogel—have contributed information generously: sharing their expert synthesis on bodies of work, offering recent insights on work in progress, or providing guidance on other aspects of preparing this Guide.

This is certainly a collaborative effort.

Chapter 1

Introduction

> “*The history of plant and animal introductions is littered with catastrophes. [Reports] concerning the implications of moving genes between populations suggest that caution is needed here also.*”
>
> Moore 2000

Context and Objectives

Two trends have made revegetation and restoration projects on public lands increasingly sophisticated and information-demanding: i) changes in public values require that more attention be given to supporting biodiversity and maintaining natural processes (Richards et al. 1998); and ii) an explosion in restoration-related research and publications has heightened concern about the negative impacts of translocating plant materials and has created a myriad of information sources (Hufford and Mazer 2003, Manel et al. 2003). For public lands managers, the decision-making process for revegetation projects goes beyond selecting the species. The lesson of “plant natives” is now broadly accepted and often required by law or policy. Exclusive planting of native plant species and removal of exotic species is now common practice in parks, forests, and natural areas, and increasingly common and encouraged in roadside treatments (for example, Harper-Lore and Wilson 2000). However, the second and equally important step is selecting the genetically appropriate population or seed source. The USDA Forest Service has long recognized the importance of this decision for commercially significant forest tree species and has made large research investments in understanding the local adaptations and tolerances of those trees, translating that information into seed transfer zones. The biological principles and issues are relevant to all native plant species, and not only the trees. The decision about appropriate genetic source for plant species is critical to both the success of the restoration or revegetation project and the long-term environmental value of the restored site. Furthermore, this genetic decision-making step is essential whether wild seeds, plants propagated from wild-collected seed (such as rooted cuttings or seedlings), direct transplants from a source population, or selected agricultural lines of native seeds are used.

Genetically appropriate choices regarding the introduction of plant materials consider both the quality and quantity of genetic diversity. The appropriate amount of genetic diversity is determined in relation to the species and the project area, and is addressed by appropriate sampling. The quality of genetic diversity refers to the issue of matching the diversity appropriately to the site to address local adaptations and the natural patterns in the species' genetic diversity.

Planting projects are opportunities to have positive or negative impacts on preserving the genetic diversity of native plant species. Indeed, some view the genetic source decision as being on par with species selection in that bad genetic choices can have consequences that could rival those of bad species choices such as introducing exotic invasive species (Moore 2000). The consequences of bad genetic choices, though, may be slower to be manifest, often are less well recorded, and may be more difficult to diagnose.

A rationale for this Guide is that the genetic principles that have informed decisions concerning appropriate seed sources for commercially important forest tree species can also be applied to such decisions for other native plant species. Some land-managing public agencies and organizations do have policies that strive to protect genetic diversity by recommending or requiring the planting of genetically local material (Box 1). However, even when there is such a policy there may not be guidelines that are sufficiently specific or flexible to guide individual planting projects. And in many other situations, there is no such policy in place or the most appropriate genetic materials may not be available.

The overall objective of this Guide is to increase awareness about the implications of managing for genetic diversity in native plant species and to provide decision-making support and tools for choosing genetically appropriate sources for planting projects. Towards meeting this objective, the importance of genetic diversity in native plant populations is explained, the genetic principles underlying the concepts of genetically local and genetically appropriate seed sources for native plants are described, tools for assessing biological value and risk in using non-local or mass-produced plant materials for large projects are provided, and illustrations of these concepts are offered with case studies involving native (US) plant species. In preparing these descriptions and tools, we have incorporated the most recently developed patterns of genetic diversity and understanding of its role in long-term plant population viability and species interactions.

Scope of Guide

In this Guide, the focus is the under-serviced area of the genetic aspects of choosing different sources of plant materials. This is only one aspect of the spectrum of decisions involved in revegetation projects (Figure 1.1). In general, decisions for site preparation, species selection, seral stage considerations, or most of the establishment, management, and monitoring activities are beyond the scope of this Guide. Many of these decisions are informed by the rapidly expanding field of restoration science, and much literature and large compendia of information are available (for example, CNAP 1998; Gobster and Hull 2000; Perrow and Davy 2002a, 2002b). Furthermore, the Guide does not cover all the genetic considerations or consequences of every type of planting (or seeding) project, but focuses on the large-scale revegetation projects that are considered after fires or mechanical overstory removal. However, the genetic principles presented here also apply to other—smaller-scale or alternative objective—situations, but there may also be additional considerations in those projects that have not been covered here. For example, rehabilitation on a former mine site may require selection of plant materials that tolerate the degraded site status, or may require several stages of planting—using different species to achieve specific results at each stage. In that situation, the genetic source may not be the primary, or at least initial, consideration. Similarly, in wetland or riparian restoration projects, many of the same principles and recommendations provided in this Guide will apply, but there may be other considerations related to restoring slope stability, water quality, or habitat values that may alter the priority of addressing genetic considerations.

Most of the descriptions and context for these guidelines are based on widespread or regionally restricted native plant species, rather than those that are endangered. Good resources are available elsewhere for exploring the special needs and restoration approaches for rare or endangered plant species (for example, Falk and Holsinger 1991, Falk et al. 1996). The focus here is also on flowering plants and conifers rather than spore-bearing vascular plants and non-vascular plants.

Because the focus is on genetic variation *within* native species, reference is made to definable units or taxa at various subspecific levels, including subspecies, populations, ecotypes, and genotypes. And because domesticated derivatives of these units are used in planting projects, horticultural varieties and selected lines and cultivars (that is, agricultural releases) are also included in the discussion. Although it is not explained how to build a plant list for specific projects, there is some discussion on how to examine initial lists for genetic appropriateness of available plant materials. This may provide another tool for refining plant lists through removal of some species or substitutions of others.

Biodiversity and Genetic Diversity

There have been many definitions of biological diversity (hereafter referred to as biodiversity). An often-used definition is “the variety and variability among living organisms and the ecological complexes in which they occur” (OTA 1987). However, as pointed out by Noss (1990), this definition fails to include the processes—such as interspecific interactions, natural disturbances, and nutrient cycles—that are so critical to maintaining biodiversity. He suggested that rather than trying to define biodiversity, it might be more useful to characterize it in a way that recognizes the scope and nature of the term. He suggested a hierarchical characterization that communicates that each level in the hierarchy affects, and is affected by, the other levels. The four hierarchical levels of organization that he suggested as a characterization of biodiversity are: 1) regional landscape; 2) community-ecosystem; 3) population-species; and 4) genetic (Noss 1990). The Forest Service has recognized these four levels of biodiversity (see, for example, Franklin et al. 1981). This hierarchical representation of both the structures (such as ecosystems and species) and processes (such as pollination and natural selection) that comprise biodiversity is depicted in Figure 1.2.

Genetic diversity is the variation in deoxyribonucleic acid (DNA) among individuals (and populations and species). As the basis of the biodiversity hierarchy, it can be understood that anything that compromises genetic diversity will have cascading effects that could negatively impact biodiversity. Its fundamental difference from other kinds of variation (such as differences among individuals that result from growth in different environments) is that it is passed down from generation to generation. In contrast, species-level diversity (or diversity among species) emphasizes the number and type of species present in a given geographic area, regardless of the type or amount of genetic diversity present within each species. Genetic diversity is the means by which species can become linked or adapted to their environments, including other organisms (such as pollinators) with which they may co-evolve. As such, and in the face of perhaps accelerated changes in climate, genetic diversity is a critical component to the long-term survival of native plant species. Management of native species and ecosystems, therefore, requires not only habitat conservation but genetic conservation—providing the best opportunity, given current information and understanding of the species' biology, to maintain the species' adaptive potential and the patterns and levels of genetic diversity that are within the normal range for the species. While the direct loss of genetic diversity is most often associated with major loss of habitat and shrinking populations, the loss of genetic integrity can result from management activities, particularly those associated with planting. Genetic integrity, as defined here, refers to the quality and arrangement of genetic diversity—within individuals and across the landscape—in relation to natural processes. It thus reflects changes in genetic composition caused by local adaptive pressures and other processes that can influence the mating success and survival of individuals.

In general, plant species are more genetically variable than animal species. One reason for this is the necessity for plants to meet environmental challenges in place, whereas animal species have the additional advantage of mobility and other behavioral mechanisms for accommodation (Table 1.1). In general, animal species are less likely to hybridize with other species and less tolerant of genetic aberrations than plant species. These and other characteristics underscore the genetic diversity and complexity of plant species.

Genetic conservation efforts are ideally conducted in a proactive manner, before the genetic resource is so depleted as to leave few options for recovery and before it has lost significant current and potential adaptations. As such, establishing *in situ* genetic reserves for native plant species is an important practice—both to serve as natural arenas in which the species can continue to adapt to changing environmental conditions and to provide sources for seed collections for restoration projects (Box 2). It is difficult to sense the urgency of such action, however, because the loss of adapted combinations of genes is cryptic, and effects may not be obvious to us for many years, especially in long-lived species. Genetic integrity can often be severely degraded without an immediate loss in the census number of individuals in a population, or an obvious loss of genetic diversity, as measured by some common genetic statistics. Hence these losses are called "secret extinctions" (Ledig 1991). Thus, the high survival value of genetic integrity to native plant species is undermined by the invisibility of loss of genetic integrity, at least at early stages.

What are appropriate genetic sources?

Appropriate genetic sources of plant materials for revegetation projects are those that conserve the natural genetic condition of the target plant species. The natural genetic condition includes the amount of genetic diversity in the range of the species affected by the project, the special nature or local adaptations of the species within this range, and the processes (including pollination, seed dispersal, etc.) that maintain and influence genetic diversity. But just as what is appropriate in a political or social sense changes with context, so too does what is genetically appropriate. That is, it can't be simply quantified or defined in a way that suits all situations. What is genetically appropriate will vary from species to species, and sometimes even from one area to another for the same species. That is why it is important to understand the general nature of genetic variation and develop informed rationale for making these decisions. It is always a subjective decision and one that is better served with science. What is genetically appropriate may change or become more clearly defined, with the advent of new research. Consequently, a professional land manager should aggressively pursue the results of new research—particularly, genetic research on species of concern or those that are often involved in revegetation projects. Finally, although the attention or priority given to genetic issues may change with management objectives, what is genetically appropriate does not change with country or administrative boundaries.

Why choose appropriate genetic sources?

The reasons (and hence, need) for carefully selecting the appropriate genetic source for planting projects involving native species are numerous. The following reasons can be identified, which can be broadly classified as concerns related to the species' viability, the broader ecological community, and management interests.

Species' viability:

1. ***Provides potential for future survival of the species.***

   Genetic diversity is one of the pillars of long-term species survival. It provides variations in species' traits such as growth rate or temperature sensitivity, so that even as the environment of a species changes, there may be some individuals that are well-suited to the new conditions. Genetic diversity may also provide the 'right stuff' for a species to become established in new habitats. Thus, over both space and time, genetic diversity provides some insurance towards continued survival. There are various measures of both genetic diversity (for example, heterozygosity) and fitness or long-term survival potential of a species. One example of the relationship between these two general values is found in a recent study by Reed and Frankham (2003). Their analysis of over 30 genetic studies of various species revealed a highly significant and positive relationship between the species' fitness and genetic diversity.

2. ***Affects future opportunities for the species to evolve*.**

   Maintaining the amount and quality of genetic diversity provides the basis for local adaptations to be maintained and to continue to occur in response to environmental changes. Furthermore, this genetic diversity is fundamental to the longer term processes that can lead to a new subspecies or species.

3. ***Provides appropriate genetic linkages among fragmented populations*.**

   Similar to the idea of using corridors to link suitable habitat areas for wildlife, using genetically appropriate materials in planting projects can serve as genetic stepping stones (that is, sources and sinks for pollen and seeds and other types of propagules) among fragmented populations of those species.

Broader ecological community:

4. ***Preserves historic interactions.***

   Over long periods of time, relationships among various species develop that may be significant at a within-species or genetic level. For example, certain subspecies or populations of pollinators (such as birds or insects) may be specialized to prefer certain populations of a plant species that are distinguished by a genetically-based trait such as a particular flower color or scent.

5. ***Preserves biological diversity.***

Genetic diversity is an important part of the overall hierarchy of biological diversity and is, in fact, one of the three levels of biological diversity recognized by the World Conservation Union, and one of four recognized by the Forest Service.

6. ***Minimizes the risk of inadvertently introducing a new species into the area.***

If plant species are only managed at the species level, then it is possible that occasionally look-alike species (any species, often closely related, that are difficult to distinguish based on appearance only at the time they are planted) could be inadvertently planted in lieu of the native species. However, if the specific genetic source of plant materials is considered and recorded, this would minimize the opportunity for such species-level mistakes. In addition, there is a greater risk that foreign disease or pest organisms could be introduced into an area if a genetically inappropriate (and most likely—geographically distant) source of plant material is used.

7. ***Minimizes cascading effects throughout the (ecological) community.***

If an inappropriate genetic decision is made for planting materials which results in maladaptation and ultimately failure of the revegetation project, the impacts are not confined to that particular species. Other species that interact with or depend upon the failed transplants will be stressed or even more seriously impacted. Any genetic changes that alter a given species' ecological properties are likely to be felt and magnified in the community, as much as if the species were removed or a new species were added (Endler *et al.* 2001).

8. ***Avoids potentially ill-fated hybridizations.***

Bringing geographically distant or otherwise genetically inappropriate representatives of a plant species into a new area sets the stage for within-species hybridizations that would not have been possible in nature. Although hybridization is a natural process, plant introductions may lead to combinations—not necessarily beneficial—that otherwise would not have occurred. For example, matings between distantly related representatives of a species may not be fully compatible. Or seeds from such between-location hybridizations may not be well-suited to the current environment, thus wasting reproductive output.

Management interests:

9. ***Protects project investments and minimizes financial consequences.***

Compared with site preparation, planting or broadcast seeding, fertilizing and weed control (if required), the cost of the plant materials may be a minor component of the overall project costs. To the extent that a successful revegetation project relies on using plant materials that are appropriately matched to the site, it makes good management sense to choose these materials carefully. The difference between using genetically appropriate or inappropriate plant materials may make little difference in the overall cost of the project, but may make the difference between successful revegetation and low survival. Alternatively, if the plant materials *are* a large part of the project cost, it makes sense to select and use them wisely.

10. ***Avoids the waste of valuable genetic resources.***

When seeds or other plant materials are used in a revegetation project that subsequently fails because of poor adaptive matching with the project site, the waste of those plant materials may be a significant cost. Those seed may be replaceable—but there are still costs associated with the collection and certification of these materials. At worst, the wasted seed may have been in short supply or otherwise not replaceable because the original population from which collections were made no longer exists or is genetically contaminated.

11. ***Protects federal* in situ *genetic reserves*.**

Some federal lands serve as important germplasm reserves for native plant species. Using genetically appropriate plant materials for projects that are close to (for example, within pollen distribution range) these reserves helps protect them from genetic contamination that might otherwise occur. Such genetically appropriate decisions help to preserve potentially important sources of local germplasm for plant materials development or future revegetation needs.

12. ***Demonstrates consideration of neighboring land.***

Lands adjacent to the revegetation site will also be impacted by the genetic decisions for that site if they are within seed- or pollen-dispersal distance (which can be a substantial distance for bird-dispersed seed). The management objectives and values of adjacent sites should also be respected when making decisions regarding the source of revegetation material. The safe option—which protects ecosystem values on both the revegetation and neighboring sites—is to choose genetically appropriate plant materials.

13. ***Protects research opportunities on natural systems and species*.**

Research on native plant species or their associated processes normally requires that the research site be in a natural condition with a minimum of human impact. If planting of inappropriate genetic materials has occurred, this may confuse the results, minimize the value, or even prohibit certain kinds of research.

The relevance or relative value of each of these 13 considerations will vary from project to project, and sometimes over the time course of a particular project. A quick review of the reasons for considering the genetically appropriate source of plant materials may provide a helpful perspective during a situation when time or other project resources are scarce. Minimally, this review will ensure that the project manager has made a well-considered, balanced, and justifiable decision. Potentially, it will influence choices and contribute to the long-term success of the revegetation project.

Figure 1.1. Elements of a natural area revegetation project. Shaded areas are the focus of this Guide; hatched areas are covered to some extent—specifically, the genetic aspects of the topic indicated.

Decisions Pertaining to Revegetation Projects

	Type of Activity or Decision				
		Assisted regeneration: Plant materials translocated to project site			
Situation	**Natural regeneration**	**Site preparation**	**Species selection**	**Genetic source selection**	**Establishment, Management, Monitoring**
Post-Fire	▨			■	
Post-Harvest	▨			■	

Figure 1.2. A representation of the four levels of biodiversity as viewed by the Forest Service and others. This includes both structures such as species and processes such as natural selection.

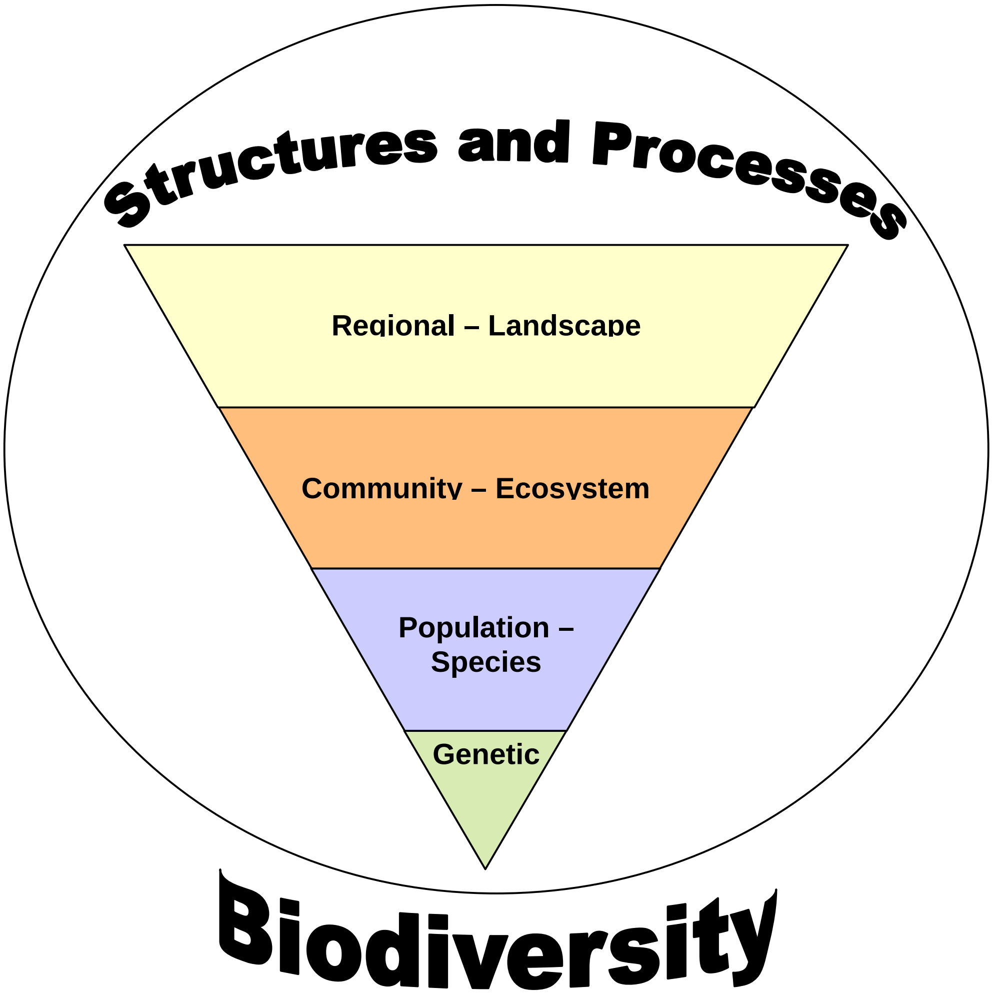

Table 1.1. Some basic differences between plants and animals in some genetic characteristics.

Trait	Plants	Animals
Location of DNA	Nucleus, mitochondria, chloroplasts	Nucleus, mitochondria
Size of chromosomes	Wide range in size, even among species within the same family	Less variation in size
Stability of chromosomes	Wide range in number, even among species within the same genus, and even among individuals or populations within the same species	More stable
Variation within individuals in chromosome number	Occasional	Extremely rare
Selfing/inbreeding	Common	Uncommon
Monoecy (Hermaphrodites)	Common	Uncommon

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Box 1: The Significance of *In Situ* Genetic Reserves

In situ reserves are areas dedicated to conserving, in the long term, species or populations within their native habitat. Their purpose includes conserving the processes and conditions that allow normal functioning and reproduction of those species. For plants, that includes conditions allowing natural pollination processes, seed production and dispersal, germination, and recruitment of seedlings or sprouts to occur. *In situ* reserves, depending on their size and situation, can simultaneously support conservation of many species. Existing *in situ* reserves, natural areas, parks, or protected areas are not necessarily genetic reserves (Neel and Cummings 2003): it depends on how they were chosen and how both the reserve and surrounding lands are managed.

In situ genetic reserves have those same objectives, plus an additional one of maintaining and protecting the genetic diversity and integrity (quality of the genetic diversity and its relationship with the environment) of the target species or populations. These are also sometimes called gene-pool reserves. Although some aspects of genetic conservation can be achieved by storing seeds or other plant propagules off-site for later use (called *ex situ* genetic conservation), *in situ* genetic reserves provide the only means by which genetic diversity can be maintained in its natural and dynamic context. This context includes the processes that maintain and shape genetic diversity over time, thereby allowing new mutations to be incorporated, and natural selection and other natural processes.

The focus here is on *in situ* genetic reserves that are chosen for the purposes of genetic conservation and for species where there is still sufficient habitat range and genetic diversity to make decisions based on principle rather than necessity. The latter situation involves species that have lost much of their habitat and diversity, and perhaps are federally or state-listed as threatened or endangered or having a USDA Forest Service designation of sensitive. In those cases, the limited size and/or number of populations often means that reserves are decided by what is available, rather than what would have been desirable for genetic conservation had the species been managed differently from the past.

Decisions about *in situ* genetic reserves center around position, number, and size. Much of the early information concerning reserves comes from animal conservation experience and research (for example, Margules *et al*. 1982, Shafer 1990). The principles remain similar, but with plants the key driving force in determining size and number is the spatial genetic structure of the species. For example, if the species of concern is a plant with several disjunct populations, all of which are strongly differentiated genetically, a manager could not represent the genetic diversity in that species with a single reserve within one population. Ideally, for comprehensive genetic conservation of a species, one would locate appropriately sized genetic reserves within each genetically differentiated population, or a sampling of less differentiated populations.

The geographic location of genetic reserves is best guided by a knowledge of within-population genetic structure, as well as other factors such as potential for buffers (that surround the reserve and buffer it from major edge effects but may allow some nondestructive activities such as ecotourism, research, or education), size required for natural processes related to natural regeneration potential, and freedom from sources of genetic contamination. The ideal process involves carefully siting the core reserves, designating buffer areas, and development of genetic management and monitoring guidelines. Discussions of the general principles and issues of *in situ* plant reserves are provided by Hawkes *et al*. (1997) and Given (1994).

An adequate size for reserves is often discussed relative to the concepts in population biology of minimum viable population or the number of individuals needed to form a self-sustaining breeding population in the long-term. And because the focus is on genetic diversity and the processes that maintain it, we need to consider not only population viability, but the amount and structure of genetic diversity in the population. *In situ* genetic reserves the more appropriate concept is effective population size (N_e). This value is *not* the actual number of plants in the population but a smaller, theoretical number based on the number of unrelated individuals, and is affected by such factors as the mating system (for example, outcrossing or selfing) of the species and gender ratio of the target population. Until recently a frequently-used rule of thumb for long-term genetic conservation was that an effective population size of approximately 500 is necessary (in other words, 500 unrelated, randomly interbreeding individuals). In the mid-1990s, the availability of empirical evidence and the further development of genetic theory led to the recommendation that the general rule for effective population size should be closer to 5,000 than 500 (Lande 1995). Translating the effective population size into a genetic reserve size requires insight into how genetic diversity is structured in the population, the age and gender profiles, life-history characteristics (life-form of the species such as herb or shrub, type of reproduction, and so on), the presence of dormant seeds in the soil, physical distances between individuals, and pollen dispersal distances. Generally, the actual or census number of individuals required is considerably larger than the effective population size (Lande and Barrowclough 1987, Nunney and Elam 1994, Nunney 1999). As a hypothetical example, in a stand of 100 quaking aspen (*Populus tremuloides* Michx.) trees (where trees are either male or female) that consists of 75 females and 25 males, the effective population size is only 19. (This estimate considers the influence of gender ratio only, and not the other factors that affect N_e).

There are few examples of *in situ* genetic reserves for plant species in the US. One high-profile example is the system of *in situ* genetic reserves for Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) in the State of Washington (Wilson 1990). Beginning in the 1980s, the State's Department of Natural Resources (WDNR) started to designate genetic reserves because of concern over genetic contamination of the natural populations of Douglas-fir. Genetic contamination was a presumed consequence of large areas being planted with genetically improved stock that were derived from a fraction of the species' natural genetic variation. WDNR was also concerned about the largely unknown effects from selection pressure due to forest management practices. Genetic reserves (areas protected from harvesting) were established according to elevation and seed zones—the latter reflecting genetic differentiation among populations. As of 1988, over 100 gene-pool reserves had been located and designated, amounting to 1,050 ha or 0.19% of WDNR forest land. These reserves were designed and selected with the best available information on the site history and local genetic structure of the species.

The Forest Service has a classification known as Research Natural Areas that is helpful in conserving genetic diversity. Although they are not specifically selected for genetic conservation values, the use restrictions (for example, no harvesting) on these areas provide some protection against unnatural disturbances.

Establishing and maintaining *in situ* genetic reserves involves challenges. Finding areas that are reasonably natural, contain appropriate levels of genetic diversity, and are relatively free from management impacts (particularly genetic contamination) is the first challenge. Providing an ongoing monitoring and management program, with suitable staff and adequate funding is the next challenge. And protecting the reserves from major losses or inadvertent human impacts is an ongoing challenge. Major losses could be in the form of fire—although, if these are natural wildfires of natural intensity and proportion, the species may not suffer genetic loss (that is, if fire-adapted, the species may have resilience, viable seedbanks, or resprouting capacity (for example, lodgepole pine (*Pinus contorta* Dougl. Ex Loud.)). However, unnaturally intense or frequent fires may be catastrophic. Significant impacts on plants within genetic reserves can also result from severe invasions from introduced plants or pathogens, or insect epidemics—both introduced and native. There are also accidental losses such as unintentional harvesting or administrative changes that may impact genetic reserves. For example, since implementation, approximately 25% of the genetic reserves for Douglas-fir in the State of Washington have been administratively lost—that is, traded or transferred to different ownership. Some of those reserves affected can still function as genetic reserves under the new ownership but the coordination and management necessary to achieve specific genetic outcomes have been lost or lessened (J.D. DeBell, pers. com.). Because of these risk factors, it is acknowledged that we need to aim for higher than a minimum number of reserves and larger than the minimum size suggested by theory (for example, Mangel and Tier 1994).

Although there are significant challenges in designing and maintaining *in situ* genetic reserves, they are irreplaceable in their function. For example, when a new commercial value in a plant species is discovered, or a species is listed as endangered after a long history of habitat loss, it becomes apparent how valuable those *in situ* genetic reserves would have been.

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Box 2: Policies that Protect Plant Genetic Diversity: A Sample from US Agencies and Organizations

Policies that favor management practices beneficial not only to species survival and ecosystem health but that maintain natural genetic diversity are being adopted at federal and local levels. Such genetic policies are now in practice for an array of US federal and state agencies that manage or regulate natural resources, environmental nonprofit organizations that own wildlands (for example, The Nature Conservancy and various land trusts) or that educate or advocate for environmental conservation, and professional societies and coalitions. Alternatively called recommendations or guidelines, they seek to inform their staff or the public about the importance of maintaining biodiversity at the genetic level and to encourage planting of genetically appropriate plant materials. Box 3 provides some information on USDA Forest Service directives directly related to genetically appropriate use of native plant species. Box 4 provides a broader context of federal acts, presidential directives, and executive orders that are relevant to native plant use on federal lands. Of course, sound scientific information is required to carry out these well-intentioned policies.

The USDI Bureau of Land Management in California approved a Supplement to their Native Plant Material Manual in 2001 that addresses the need for selecting genetically appropriate native seeds and plants for management activities including erosion control and restoration (BLM 2001). They couch this need within the broader project goals of achieving long-term plant community stability and integrity. The key policy statements in this supplement are as follows: “To the maximum extent possible, germplasm of native species that is adapted to specific abiotic and biotic site conditions shall be used in revegetation efforts. Use of non-local native, or non-native plant materials will occur only when no other feasible alternative exists, or unusual ecological circumstances dictate that their use is superior.”

At a state level, the California Department of Parks and Recreation has had a policy since 1994 that encourages planting genetically local material in restoration projects, as part of its responsibility to protect the State’s biological heritage (Woodward and Harrison 1989). The policy—drafted in the 1980s but not officially approved until 1994—states: “In order to maintain the genetic integrity and diversity of native California plants, revegetation or transplant efforts in the State Park System will be from local populations, unless shown by scientific analysis that these populations are not genetically distinct from populations being proposed for use. If local populations have been decimated, the closest, most genetically similar population (s) to that State Park System unit will be used (California State Parks and Recreation Commission 1994). This policy is interesting in its assumption that a local genetic source for planting material is biologically meaningful unless proven otherwise.

The Nature Conservancy (TNC) has prepared guidelines to assist TNC staff and volunteers with the selection and use of genetically appropriate plant stock in wildland revegetation and restoration projects (TNC 2001). As an organization that owns conservation areas, works directly with public agencies and land managers, and provides public education, their policies have influence at multiple levels. Their guidelines address the rationale for preserving genetic diversity, potential adverse impacts from planting genetically inappropriate plant material, general guidelines for selection of plant stock, and some specific guidelines for emergency (fire) rehabilitation projects, roadside plantings, and horticultural plantings. TNC guidelines emphasize the need to use local sources of plant material, the importance of planning revegetation projects well ahead to allow accumulation of adequate seed supplies, the relative biological safety of using certain sterile cultivars of exotic species rather than non-local or unknown sources of native species in emergency or rehabilitation projects, and the importance of how seed supplies are collected in the wild or increased in nurseries. At the state level, TNC may have even more specific guidelines. For example, TNC Florida’s trustees passed a “policy and criteria for species translocations to preserves” over ten years ago. This includes project review by scientific staff, protection of local genetic diversity, avoidance of a small sample size for the translocation source, and consideration of ecological and genetic impacts of the translocation on the natural community (of the translocation site) (J.M. Randall, pers.com).

The California Native Plant Society (CNPS) posted genetic guidelines on its website at about the same time as TNC, with the purpose of protecting the remaining stands of California's native vegetation from genetic degradation (CNPS 2001). Those guidelines recommend planting local genotypes of plant species for ecological restoration projects, and sterile or non-invasive plants where necessary for emergency erosion-control landscaping—later planting local sources of native plant species. For horticultural landscaping, they recommend using non-invasive exotics or known local sources for native plant species. They emphasize not planting unknown sources of native plant materials as they may not be well adapted locally, and may hybridize with local populations, undermining their adaptive capabilities to local environments.

The University of California (UC) also has public service and land management responsibilities. For its Natural Reserve System—a collection of some 34 properties comprising over 130,000 acres that were selected and are maintained for research and teaching purposes—there is an interest in maintaining the native condition of these holdings. Indeed, their value for research and teaching declines with departures from a natural condition. As such, they formed a committee to evaluate the likely impacts from introduction of non-local genotypes into UC Reserves. The reason for this evaluation was frequent requests by scientists to conduct studies on UC Reserves that involved planting or seeding with native plant material—some of which was from non-local sources. Thus, part of the rationale was to evaluate the effects from such research and part was an education effort, to inform scientists who lacked a background in genetics of the potential risks of introducing non-local plant sources into the Reserves. The posted essay (Endler *et al*. 2001) explains why introducing non-local genotypes is undesirable, with the hopes that this treatise will discourage such research practices, and encourage research that uses local genotypes where possible, or removes non-local genotypes after the research is completed. In addition to the influence of this educational effort, prospective users of the Reserves must complete a comprehensive application that reveals any potential negative impacts on the Reserve's resources—including introduction of foreign genes. Such potential effects influence the decision of whether or not the research is permitted.

A final example of genetic policy comes from a coalition of native plant societies and other native plant science conservation organizations from 28 states—The Native Plant Conservation Campaign. A project of the Center for Biological Diversity and the California Native Plant Society, this network's mission is to promote appreciation and conservation of native plant species and communities through collaboration, education, law, policy, land use, and management. In service of this mission, they encourage use of "local, genetically appropriate native plants" in revegetation projects (www.cnps.org/NPCC).

The Colorado Native Plant Society (CONPS) has adopted policies for restoration, revegetation, and landscaping that encourage the use not only of native plant species, but sources that are genetically appropriate. Specifically, their guidelines state "In large-scale rehabilitation, revegetation, and wildflower planting projects, use plant materials derived from nearby, similar habitats. CONPS stresses the importance of protecting the genetic integrity of the surrounding native species and natural vegetation. The introduction of non-local genetic material may irrevocably alter the native flora." (CONPS). In the absence of direct genetic information for defining genetically appropriate source materials, they recommend selecting plants from similar conditions (e.g., elevation, frost period, temperature) to those of the project site. They also suggest caution in using cultivars of native species. None of the comparable organizations for other Region 2 states (including the Kansas Wildflower Society, the Great Plains Native Plant Society, and the Wyoming Native Plant Society) at the time this Guide was published had policies related to maintaining or protecting genetic diversity of native plant species.

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Chapter 2

Context for Making Genetically Appropriate Plant Material Choices on USDA Forest Service Lands

One challenge in this Guide was to decide and describe which situations would be addressed in relation to normal Forest Service field activities. It was decided that the focus would be the large-scale revegetation efforts such as those associated with fires or harvests, and that all plant species (with as many examples as possible) would be included, not just those directly affected by harvests. These activities are historically significant and ongoing on Forest Service lands. They involve large areas and thus revegetation efforts potentially have meaningful large-scale impacts. It is understood that are various terms associated with revegetation following those disturbances (for example, rehabilitation, restoration, reforestation), each with a specific meaning within the Forest Service and associated with particular goals. As such, the focus for this Guide is perhaps best explained as a combination of activity and goal: that is, post-fire and post-harvest situations where the main goal is restoration.

Management decisions on most Forest Service lands involve, or have implications for, plant genetic resources. Whether through direct introduction of plants or seeds, deciding what parental plants will be left on site for natural regeneration, or by selectively encouraging or discouraging reproduction of plant species, the plant genetic resources on these lands are affected. Forest Service activities that typically or potentially include introduction of plant material, and thus have genetic implications, include:

- Postfire rehabilitation
- Postharvest seeding or planting: including not only the commercial tree species but other native plant species
- Timber postharvest revegetation of logging roads, skid trails, slash burns
- Road construction cut-and-fill slopes
- Range improvement
- Campground reconstruction

- Wildlife and fisheries habitat restoration
- Creation of wildlife or wetland habitat
- Restoration of riparian areas
- Recreational developments
- Restoration of mineral drilling pads
- Mining site bioremediation or reclamation
- Management of exotic invasive species
- Revegetation of special-use sites and corridors (such as pipelines, cable lines, electrical corridors)
- Fuel reduction projects
- Augmentation of declining rare species populations and recovery efforts for listed species
- Improving insect and disease resistance of target plant species.

The first two situations—postfire rehabilitation and postharvest seeding or planting of native plants—often have a restoration goal and are the primary focus of this Guide. They are common activities, frequently involve large areas, and often involve introduction of plant materials. Any introduction has the potential for ecological and genetic impacts to native populations and ecosystems. Federal Acts and USDA Forest Service directives related to these and to the other management actions listed here are briefly reviewed in Boxes 3 and 4.

Different agencies and organizations that manage, advocate, or provide education about natural areas often have specific understandings or definitions for the related terms such as revegetation or restoration (please refer to the glossary for definitions used in this Guide). Restoration as defined here, encompasses the ecological end of the spectrum of rehabilitation projects. It is “ecological” restoration rather than “agricultural” because the intent is to restore a disturbed or altered site by encouraging a trajectory toward a condition that emulates a previous natural condition. As in rehabilitation, the restoration process may require various levels of treatment to achieve this goal. When planting occurs, use of locally adapted plants provides insurance of appropriate adaptation and reestablishment of interactions among species that may be important to recovery of population and ecosystem sustainability. Launching a trajectory toward a set of desired historical natural conditions is often the goal, but sometimes the goal is to achieve a particular position along this trajectory, such as a certain stage of community succession. Restoration is consistent with a goal that includes maintaining native biodiversity.

The information presented in this Guide should also support projects with other goals (for example, reclamation). For example, a literature review of factors affecting the success of establishment of native shrub species on lands in the Rocky Mountains disturbed by mineral extraction indicated that use of local ecotypes, varieties, or subspecies was important (Paschke et al. 2003). Even though there may be different *initial* goals in such situations, such as bioremediation or soil stabilization, there is often a secondary objective that is closer to restoration. Similarly, revegetation in riparian areas may initially be focused on streambank stabilization, hydrological issues, or other considerations. Nevertheless, even if there is a sense of urgency about site management that may temporarily supercede a restoration objective, ultimately, one often wants to restore as much ecosystem function as possible. It is important to think ahead and avoid compromising a restoration objective in meeting other short-term objectives, to the extent possible.

With projects that don't require plant introduction, there still may be genetic implications. Plant genetic materials can arrive on site intentionally, accidentally, and naturally. Intentionally introduced genetic resources are of two kinds: those that are brought to the site and planted or broadcast (such as seed, vegetative propagules, or seedlings); or those that have been intentionally left on or near the project site as seed sources of new plants (such as selected plants or seed trees after harvest). Accidentally available genetic resources are those that are unintentionally introduced through spreading of topsoil, duff, hay bales, or other materials brought to the site that could be carriers for seeds.

Naturally available genetic resources are those that remain from the pre-existing (prior to disturbance) plant populations either on or near the disturbed site. These include seeds from canopy or soil seedbanks or dispersed from nearby populations, bulbs or corms, root systems or stems of species with sprouting or suckering ability (such as root suckering in *Populus tremuloides* Michx.), and new plants formed by branch layering from species with that ability (including some species of *Ceanothus* and *Arctostaphylos*). These naturally available genetic resources may include any exotic as well as native species that are resident to the area. Regardless of how the plant genetic materials arrive on site, it can only be helpful to be aware of the full range of potential new growth and the consequences for the desired outcomes.

The spatial and temporal contexts of postfire and postharvest management projects are important to recognize. Because there are two senses of spatial and temporal scale that are relevant to revegetation projects (that of the project and that of the plant) there are some terms and concepts that can be confusing if not recognized for their context.

In this Guide, the projects addressed are mainly those that are large in spatial size and thus would normally require some seeding or planting to augment any input from adjacent areas or expected contributions from resident seed banks. By focusing on the goal of ecological restoration, the information presented here would also serve to protect the integrity of any other adjacent natural areas or research sites, and their inherent values (see Chapter 1 for more discussion about the reasons to choose appropriate genetic sources).

Matters of spatial scale

There are two relevant spatial scales here: one is the spatial scale at which the plant species genetically varies; the second is the spatial scale of the project—which could be thousands of acres to less than an acre in size (Table 2.1). The former scale can also be quite variable; that is, a plant species may have rather uniform genetic variation over large areas in some parts of its range, but then vary over finer spatial scales in other parts, often as a reflection of the differences in environment over different parts of its natural range. Introducing plant genetic materials to the restoration or rehabilitation site could be considered a challenge of matching the plant's genetic spatial scale to that of the project site. Some of the terms will be introduced here that are used in describing the spatial genetic scale of plant species. This topic will be discussed in more detail in Chapter 4.

For the plant species, the largest spatial level is the species' range, the entire geographic range over which a species naturally occurs. Variations on this definition are encountered when one extends range to include the historic range of a species (where it once, but may no longer occur). Sometimes range is also described in ecological or even physiological terms. In those cases, rather than using geography or physical maps, the environmental attributes are described that characterize the species habitat (such as elevation, soil type, or associated plant species) or its physiological limits (for example drought or frost tolerance which often vary by a population's elevation, latitude, longitude, or some combination thereof). Next, the region is usually part of a species' range, consisting of a set of local populations. Region is variously and loosely defined, but is often used to describe some smaller part of a species range. However, with some plant species with particularly limited ranges, the region may delimit the entire range of a species. See Figure 2.1 for some examples of different spatial scales of species genetic diversity relative to project area.

Finally, local population refers to the smaller unit of the species. Within the discipline of genetics, a technical definition of population is a group of individuals of the same species living within a sufficiently restricted geographical area that any member can potentially mate with any other member (assuming they are a sexually reproducing species, and that members are of opposite sexes) (Hartl 1988). This definition is less appropriate for plant species that reproduce asexually or that can only mate with a subset of any population because of genetic incompatibility mechanisms. The term local population (also called the deme or subpopulation) is used for the actual interbreeding unit. That is, because of environmental barriers or variability that can affect reproduction, limitations in pollen dispersal distance, or other factors, the larger population that in theory can interbreed amongst its members, in fact may have more local structure for most of its reproductive activity. There are situations, though, where a population is the same as a local population. Because it is the arena within which most of the mating and inheritance occurs, the local population is the fundamental genetic unit of a species. It is this unit that adapts and evolves.

A local population, using the genetic definition, is often difficult to define in the field. It is really more of a theoretical concept—one that is important because it refers to the spatial scale at which genes are carried in pollen or seeds (or perhaps in rootable branches or rhizomes in some asexually reproducing species). Only if a plant population is well defined and very distant from other populations would it be easy to point to group of plants in the field and confidently assert they were one local population. Sometimes there is confusion in restoration discussions when the term "local" is used to refer to the project spatial scale instead of the species' genetic spatial scale. It should be clear that a local population of one species can represent a much larger or smaller area than that for a different plant species. So "local population" really has no standard geographic equivalent. Other points of confusion or controversy arise when the spatial genetic structures of individual species are not taken into account, or one tries to generalize towards restoration standards for all species and situations (Kaye 2002). Although some generalization necessarily is invoked in the absence of adequate genetic information for all species, it is important to generalize or draw inferences appropriately (based on biological similarities among species, rather than political jurisdictions or other structures), to stay mindful that the information is a generalization only, and to be ready to incorporate more specific information as it becomes available.

Although the concept of the "local population" is difficult to apply from theory to practice and is a dynamic entity, we can nevertheless make good use of this concept to make more science-informed decisions. Chapter 4 will also describe in more detail how genetic variation within populations and species can be arranged spatially and how to detect such spatial genetic structure. By being aware of the concepts of how genes of different types move about within species and have local spatial structure, by knowing that this scale will vary for different species, and by considering how the spatial scale of a Forest Service project might relate to the spatial scale of a species' genetic structure, appropriate and context-specific decisions can be made that avoid the use of controversial concepts or jargon.

Temporal context

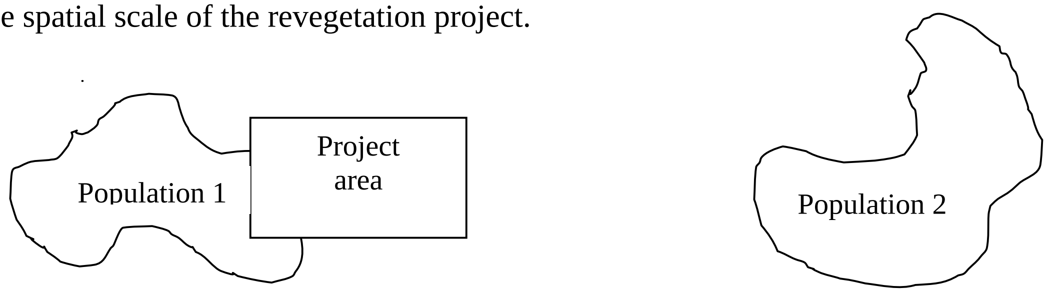
Just as spatial scale is critical to consider in activities that involve genetic choices, so is the temporal context or timeframe. Here, two timeframes are important (Table 2.1).

The first is the management timeframe: the sense of urgency associated with some projects or project goals, windows of opportunity (financial, regulatory requirements, staff-related, or biological), or the need to establish some onsite vegetation within a certain time period. For example, there could be a need to protect the investment in site preparation before the site is invaded by undesirable vegetation. Management time scales can range from almost immediate to several years after the disturbance event.

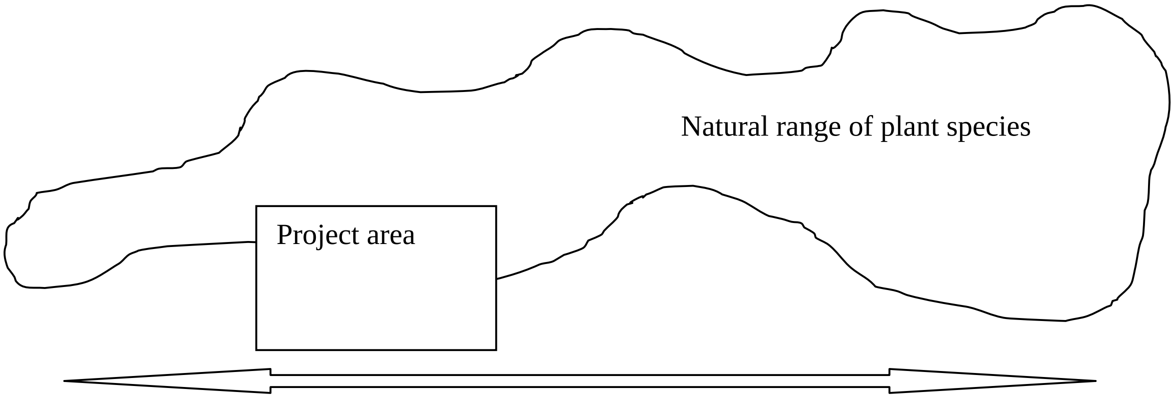
Then there are the time scales associated with the plant genetic materials themselves—both those plants that may be brought to the site and those existing on or near the project site. One important aspect of the temporal context for genetic materials is that change is always happening, it is a continuum. For example, although there may be a seed collection event that takes a sample of the genetic diversity of a plant species, and then is used in a planting project, the diversity that was initially sampled has probably changed somewhat by the time it reaches the field. This can be due to nonrandom mortality—influences such as the seed storage, seed dormancy and germination requirements during agricultural increase of seeds, nursery management practices, or even transportation conditions that result in differential germination, survival and death of plants based on their genetic differences. Genetic changes also continue on a site after the disturbance, regardless of management activities. This is one of the reasons for seed collection guidelines that refer to a minimum number of parent plants to be used for the sample. That is, seeds in seedbanks or canopy banks may germinate, seeds and pollen arrive from neighboring areas, and so on. Kozlowski (2002), for example, describes the dynamic process of natural regeneration in forests that have been harvested or disturbed. He identifies four sequential stages (stand initiation, self thinning, understory regeneration, and steady-state) during each of which natural selection is shaping the genetic diversity of the plant populations.

And finally, after the designated seeds or plants are installed on site, they continue to be influenced. Natural selection occurs as natural environmental processes continue to cause differential survival and reproductive rates among plants of different genetic composition. So the decision of when, whether, or how to provide genetic materials should take into account the genetic influences that have occurred on site after disturbance, the genetic component from naturally existing or accidentally introduced plants, and the ongoing effects of natural selection. Regardless of whether genetic diversity is a direct or high-priority project goal, there are ongoing dynamics that affect genetic diversity and that will, at least in the long term, have some impact on the project outcome regardless of whether planting or direct-seeding is employed. Genetic choices are rarely about absolutes or certainties. Appropriate genetic choices increase the probability of a successful project and help to mitigate negative consequences.

Figure 2.1. Examples of how the spatial scale of genetic diversity within a species may relate to the spatial scale of the revegetation project.

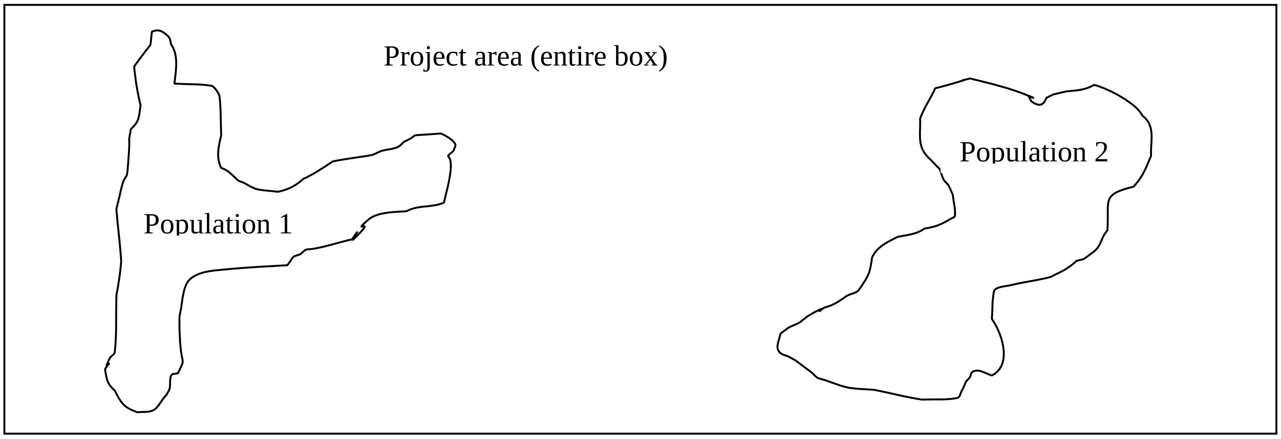


A. Plant species consists of two geographically distinct and genetically differentiated populations. Project area covers just one part of one of the two populations.



Elevational gradient. Genetic diversity in the plant species varies continuously with this gradient.

B. The plant species' natural range is large relative to the project area. Genetic diversity within the species varies continuously along an elevational gradient. The project area is small relative to the total range of the species and just involves a small elevational band of the species.



C. The project area is large relative to one of the native plant species. The entire plant species consists of just two populations, both within the project area. This situation is probably rare and would most likely occur only with species that are rare or endangered.

Table 2.1. Spatial and temporal scales relevant to plant introductions in revegetation projects.

	Levels	
Scale	**Plant species**	**Project management**
Spatial	Genetic variation within the species (species' range, region, population, etc.)	Project size
Temporal	Genetic timescales (loss of genetic diversity from seedbank, natural selection on site, etc.)	Management timescales (urgency to act, financial opportunities, etc.)

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Box 3: USDA Forest Service Directives Related to Genetically Appropriate Native Plants

Federal Acts of Congress (Acts) and Presidential Executive Orders (EO) direct or authorize Federal land management agencies to carry out particular programs and responsibilities. Forest Service Directives incorporate the actions necessary for the Forest Service to comply with these requests. "The Forest Service Directive System consists of the Forest Service Manual and Handbooks, which codify the agency's policy, practice, and procedure. The system serves as the primary basis for the internal management and control of most programs and the primary source of administrative direction to Forest Service employees" (USDA Forest Service 2002). Currently, Forest Service Handbooks exist only for woody species (see FSH 2409.17 and FSH 2409.26f below). Many native species are herbaceous, but the logic of the directives for woody plants can often be applied more generally. Here we describe the status of Forest Service Directives with respect to the source and genetics of native plants in general in the context of an internal Forest Service report on authorities related to revegetation/restoration (Austin 2001). The report points out that Forest Service Directives do not contain a section on native plants and otherwise do not include the detail needed to guide users nationally and regionally regarding the appropriate use of most native plants. This guide aims to increase the ability of practitioners in their appropriate genetic use in R2, but includes information sufficiently general to be useful to other regions too.

Forest Service practices surrounding use of genetically appropriate native trees for reforestation began in the 1930s and policy became established in what is now the Tree Improvement Handbook (FSH 2409.26g), Seed Handbook (FSH 2409.26f), and the Reforestation Chapter 2 in the Silvicultural Practices Handbook (FSH 2409.17). FS policy governing non-tree species of native plants emerged in 1993 after a series of Acts and EOs (see Box 4) directed increased use of local or genetically appropriate native plants for planting projects. Subsequently, policy regarding the use of native plants was incorporated into the Forest Service Directives System (FSM and FSH). This incorporation was consistent with the diversity and conservation mission of the Forest Service. "The United States Government Manual" (95/96), says as set forth in law, the Forest Service "mission is to achieve quality land management under the sustainable, multiple-use management concept to meet the needs of people" (USDA Forest Service 2004). However, the genetic policy for native plants remains vague, sometimes region-specific, and buried under various Titles and Chapters. No USFS handbook exists for native plants. The fragmented treatment is confusing, sometimes contradictory, and open to diverse interpretation. This will soon be fixed. The Forest Service is currently developing policy and strategy to guide implementation of a native plant program. A new section to the FSM, 2070—Biological Diversity Native Plant Management—is under development (W. Owen, pers. com.). In addition, a revision of FSH 2409.26f–Seed Handbook, Chapter 300 – Seed Source Selection, will also be available soon (M. Mahalovich, pers. com.).

Citations from the Directives (posted as of September 2004), for Service-wide and Region 2, regarding the use of native plants with respect to their genetic source are detailed below.

FSH Title 2400, Timber: Seed Handbook R2 Amendment 2409.26f-93-1, Effective 6/15/93. Seed Handbook, Chapter 200, Seed Source and Identity Control. This chapter refers to woody plants. It states "To meet management objectives, use of source-identified seed from the proper origin is required. Through time, plant species have developed in response to local environmental variables including soils, temperature and precipitation regimes, fire, insects, and diseases. Consequently, local seed is usually best adapted to local environments. In most instances, only seed of local origin will be used. In situations where research and/or administrative studies have shown that seed sources of nonlocal origin will perform better than local seed sources, seed of proven, nonlocal origin can be used." This chapter also designates use of seed zones. "Tree and shrub species in Region 2 grow under a wide range of environmental variables. Seed collection zones are geographic subdivisions within the Region encompassing areas of similar environmental conditions. The purpose of zoning is to ensure use of seed compatible with the environment in which it is to be grown. Region 2 has been zoned for tree and shrub seed collection. Seed zone maps for the Great Plains states are included in USDA Forest Service Research paper RM-150" (Cunningham 1975). The handbook further states "all plant reproductive materials (seed, seedlings, wildings, and cuttings) collected and used for revegetation projects on National Forests are to be source-identified (FSM 2475.23). Source identity of all tree, shrub, and other plant reproductive materials must be maintained from time of collection through final use in revegetation projects including storage, nursery and greenhouse production, planting records, and site records." For more about seed zones, see Chapters 6 and 9.

FSH Title 2400, Timber: 2409.17, Silvicultural Practices Handbook. Chapter 2 – Reforestation. This FSH deals with trees, but many of the concepts are suitable for other plants. Chapter 2, section 2.32 - states that failure to consider critical factors may result in regeneration failure and waste of funds. Seed source is described as a critical factor under paragraph 2. Logistical Factors: "b. Seed Source Availability. Evaluate both natural and artificial seed sources for the site for genetic quality. Seed from the site or from nearby sites is usually adapted to the site. However, the species must match the successional stage of the site. For example, early seral species require an open-grown, early successional condition and may not establish and grow in later successional stages. Seed source of planted seedlings shall be consistent with seed transfer guidelines described in FSH 2409.26f, Seed Handbook."

"Evaluate the history of old plantations before considering them as a suitable seed source. Some older plantations were planted with off-site trees and are now of seed-bearing age. Off-site trees may have been from sources hundreds of miles away or they may have been from a local area but the wrong elevation zone. Off-site trees should be removed (harvested) whenever possible to avoid further seed and pollen contamination of the area."

FSH Title 2500, Watershed and Air Management, Burned-Area Emergency Rehabilitation Handbook WO Amendment 2509.13-95-7, 1-12-95. 26.1.1. This states "Considerations for revegetation treatments include:.. a. The target area to be revegetated. b. A seed mix of species known to be effective for erosion control, adapted to the target area and compatible with future management objectives." 26.6.4 states for Burned-Area Emergency Rehabilitation (BAER) in Wilderness Areas: "Protect the genetics of endemic plants in wilderness. Choose a short-lived ground cover that will not hybridize with local species, displace a native species permanently, or offer serious long-term competition to recovery of local plants."

FSM Title 2500, WO Amendment 2500-2000-2, 5/25/00. 2523.2 - Burned-Area Emergency Rehabilitation (BAER), paragraph 2.a., Plant Materials, states "Natural recovery by native species is preferred." Paragraph 4 explains there needs to be compatibility with Forest Plans to "Ensure that treatments do not conflict with desired conditions or with ecosystem health and biological diversity" and to "Include native plant materials when possible to meet the objectives of the burned-area emergency rehabilitation. When practicable, use seeds and plants in burned-area emergency rehabilitation projects that originate from genetically local sources of native species. When native materials are not available or suitable, give preference to non-native species that meet the treatment objectives, are nonpersistent, and are not likely to spread beyond the treatment area."

FSM Title 4000, Research, WO Amendment 4000-94-2, 5/4/94. Zero code 4060 - Research Facilities and Areas, 4062.5. States "Management plans must include fire, insect, and disease protection measures and must include natural resource guidelines to protect experimental forests and ranges from activities that would reduce their research value." (FSM 4051.21f); 4063 - Research Natural Areas, states "Research natural areas (RNAs) are part of a national network of ecological areas designated in perpetuity for research and education and/or to maintain biological diversity on National Forest System lands. Research natural areas are for nonmanipulative research, observation, and study"; and 4063.02, Objective 2 and 3 state "Preserve and maintain genetic diversity" and "Serve as control areas for comparing results from manipulative research." This biological diversity element for Research Natural Areas (RNA) makes an implicit requirement that they be buffered from management practices outside their boundaries that could undermine their ability to serve as "control" areas for genetic diversity. Research Areas and Experimental Forests are on National Forest System lands, so all activities must be consistent with National Forest land management plans and approved at the local level.

The combined message from the directives. Together, these Forest Service Directives promote biodiversity and the planting of genetically local native plants. In the case of RNA's, the planting of non-local genotypes is prohibited. What prompted Federal policy and the Forest Service mission to be compatible with increased use of native plants, achievement goals for their use, and standards for their use? Richards, Chambers, and Ross (1998) described the debates and changing social values responsible for the change, much of which was rooted in a public mandate for conservation and maintenance of biodiversity. Later in April 2002, the U.S. Department of Agriculture together with the U.S. Department of Interior submitted a Report to Congress (USDI and USDA 2002) concerning supply of native plant materials for restoration and rehabilitation on Federal Lands. That document also provided a brief history of Federal programs involving native plant research and production. Furthermore, it recommended research needed for better understanding the ecology, genetics, and growing requirements of native species to increase the diversity of genetically appropriate plant materials and availability for restoration and rehabilitation. These needs included: local and regional assessments of critical desirable plants; stable funding for programs to establish plant materials; a trained workforce; seed transfer guidelines (2-dimensional in scope) and seed transfer expert systems (3-dimensional in scope); strict tracking of seed provenances; assured economical source and quantities of plant materials; seeding equipment appropriate for native seeds and rough terrain; and adequate seed storage. An increase in ecological-genetic research required for building seed-transfer guidelines will, no doubt, result in stronger and less ambiguous Forest Service Directives pertaining to genetically appropriate use of native plants. Such research will be invaluable in updating this guide and Directives.

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Box 4: Federal Acts, Presidential Directives, and Executive Orders Related to the Use of Native Plants

The following Federal Acts, Presidential Directives, Executive Orders, and Presidential Memos influenced Forest Service Directives (see FSM and FSH Titles in Box 3) that prioritize the use of native plants over that of exotic species, and the use of local and appropriately adapted native plant populations. The FSM provides a more detailed list of Acts influencing FSM Title 2500- Watershed and Air Management (Amendment No. 2500-97-2). Richards et al. (1998) and Monsen and Shaw (2001) also provide a partial listing of influential Acts and EO's. The US Code can be searched on line by name of particular Act (see US Code 2004). For Code of Federal Regulations see CFR (2004) and for Executive Orders, see EO (2004).

Multiple-Use Sustained-Yield Act of 1960 (MUSY 1960). Authorizes and directs "that the national forests be managed under principles of multiple use and to produce a sustained yield of products and services, and for other purposes." This required the Forest Service to manage for wildlife habitat and recreation in addition to extractive resources. Critical habitat for wildlife would be potentially planted with native species rather than exotic species.

National Environmental Policy Act of 1969 (42 USC Sec. 4321, NEPA 1969) as amended (1970, 1975, 1982). This Act declared a national policy which "will encourage productive and enjoyable harmony between man and his environment; to promote efforts which will prevent or eliminate damage to the environment and biosphere and stimulate the health and welfare of man; to enrich the understanding of the ecological systems and natural resources important to the Nation; and to establish a Council on Environmental Quality." NEPA laid the foundation for a coherent national approach to the environment by requiring the integration of environmental quality concerns through public participation into Federal policymaking and decision making. Through NEPA, all Federal agencies consider the environmental impacts of proposed actions

Endangered Species Act of 1973 (ESA 1973), amended 1978 (ESA 1978). This Act provided a "means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve the purposes of the treaties and conventions set forth in subsection (a) of this section." This required Federal government agencies to provide conservation programs to help remove rare species from the danger of extinction.

Federal Noxious Weed Act of 1974 - Act of January 3, 1975. (P.L. 93-629, as amended, 81 Stat. 2148; 7 U.S.C. 2801, 2801-2814) - Management of Undesirable Plants on Federal Lands - "*undesirable plants* means plant species that are classified as poisonous, injurious, exotic, noxious, harmful, or undesirable, according to Federal or State law….. It is the Forest Service's obligation to work together with other agencies to target and prioritize undesirable plant species or groups of species to be controlled or contained within a specific area. The integrated management system, which includes preventive measures, should be described."

7CFR650.23: Part 650 Compliance with NEPA, Subpart B-Related Environmental Concerns, Sec. 650.23 Natural Areas. This Code of Federal Regulations for the Natural Resource Conservation Service states "(3) Natural areas are established and maintained for a variety of purposes including:... (v) Serving as a genetic base for native plants and animals. Natural areas may be established to preserve examples of land and water ecosystems with their full range of genetic diversity of native plants and animals including threatened and endangered species."

National Forest Management Act of 1976 (NFMA 1976). This act amends the Forest and Rangeland Renewable Resources Planning Act of 1974. It strengthens references pertaining to suitability and compatibility of land areas, stresses the maintenance of productivity and the need to protect and improve quality of soil and water resources, and avoid permanent impairment of productive capability of the land. This act governs the development of forest plans that guide all resource management activities on national forests under the principles of the Multiple-Use Sustained-Yield Act of 1960. Sect. 6(g)(3)(B) directs the FOREST SERVICE to: "provide for diversity of plant and animal communities based on the suitability capability of the specific land area in order to meet overall multiple-use objectives, and within the multiple-use objectives of a land management plan pursuant to this section, provide, where appropriate, to the degree practicable, for steps to be taken to preserve the diversity of tree species similar to that existing in the region controlled by the plan." This Act governs the development of forest plans that guide all resource management activities on national forests under the principles of the Multiple-Use Sustained-Yield Act of 1960.

USDA Regulation 9500-4 (USDA 1982). This Departmental Regulation specifically tied plants to the practice of managing habitat for fish and wildlife. “A goal of the Department is to improve, where needed, fish and wildlife habitats, and to ensure the presence of diverse, native and desired nonnative populations of wildlife, fish, and plant species, while fully considering other Department missions, resources, and services.” It further states “Habitats for all existing native and desired non-native plants, fish, and wildlife species will be managed to maintain at least viable populations of such species. In achieving this objective, habitat must be provided for the number and distribution of reproductive individuals to ensure the continued existence of a species throughout its geographic range.”

36CFR219.27, Title 36, Ch. II, Sect. 219.27.(a)(5). “Provide for and maintain diversity of plant and animal communities to meet overall multiple-use objectives, as provided in paragraph (g) of this section;”… (g) “Diversity. Management prescriptions, where appropriate and to the extent practicable, shall preserve and enhance the diversity of plant and animal communities, including endemic and desirable naturalized plant and animal species, so that it is at least as great as that which would be expected in a natural forest and the diversity of tree species similar to that existing in the planning area. Reductions in diversity of plant and animal communities and tree species from that which would be expected in a natural forest, or from that similar to the existing diversity in the planning area, may be prescribed only where needed to meet overall multiple-use objectives.”

Surface Mining Control and Reclamation Act of 1977 (SMCRA 1976). Requires that a “diverse, effective, and permanent vegetative cover of the same seasonal variety native to the area of land to be affected and capable of self-regeneration and plant succession” be established. This resulted in an increase in use and demand for native plants.

EO 11987 on Exotic Organisms. 1977. President Jimmy Carter mandated the Secretary of Interior and Secretary of Agriculture to restrict the use of introduced species and to encourage the use of native species. Revoked in 1999 and replaced by EO 13112 (see below).

EO 11514 of March 5, 1970, as amended by EO 11991, May 24, 1977. This order states that the Federal Government shall provide leadership in protecting and enhancing the quality of the nation's environment to sustain and enrich human life. This order provides for monitoring, evaluation, and control on a continuing basis of the activities of each Federal agency so as to protect and enhance the quality of the environment.

Presidential Memo, April 26, 1994 (Clinton 1994). In addition to directing water conservation practices and prevention of pollution, President Clinton directed Federal Agencies, for practices at Federal facilities and federally funded projects, where cost-effective and to the extent practicable, to “(a) use regionally native plants for landscaping; (b) design, use, or promote construction practices that minimize adverse effects on natural habitat… and (e) create outdoor demonstrations incorporating native plants, as well as pollution prevention and water conservation techniques, to promote awareness of the environmental and economic benefits of implementing this directive. Agencies are encouraged to develop other methods for sharing information on landscaping advances with interested nonfederal parties." The use of native plants gained momentum following this memo which logically followed the series of Federal Acts and policies aimed at reducing noxious weed invasions and maintaining biodiversity and a healthy environment.

EO 13112 on Invasive Species, February 3, 1999. As part of the strategy to control invasive species, President Clinton directed Federal Agencies to "provide for restoration of native species and habitat conditions in ecosystems that have been invaded."

National Fire Plan 10-year Comprehensive Strategy 2000. The primary purpose of this Plan was to restore and maintain fire-adapted ecosystems.

Healthy Forest Restoration Act 2004. This Act followed implementation of the National Forest Plan and the Healthy Forest Initiative. It declares six purposes. The first three address reduction of fire risk and impacts of fire, funding for risk reduction, and protection of watersheds. The sixth purpose is "to protect, restore, and enhance forest ecosystem components—(A) to promote the recovery of threatened and endangered species; (B) to improve biological diversity; and (C) to enhance productivity and carbon sequestration." No details are provided within the act to guide restoration activities. However, practices that protect and restore ecosystem components and biodiversity necessarily include a genetic component.

Under Sec. 301, Purposes, it states "(2) to encourage landowners to maintain tree cover on property and to use tree plantings and vegetative treatments as creative solutions to watershed problems associated with varying land uses; (3) to enhance and complement forest management and buffer use for watersheds, with an emphasis on community watersheds; and (6) to maximize the proper management and conservation of wetland forests and to assist in the restoration of those forests." Restoration of the natural condition using appropriate native plants and sources is implied, but explicit direction on genetic source is lacking.

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Chapter 3

Genetic Impacts of Natural versus Artificial Regeneration

Areas that are being managed to conserve biodiversity and protect ecosystem health may no longer be subject to harvesting activities are still vulnerable to landscape-level disturbances such as fire. And sometimes there is a change in management goals for an area, such as shifting to more emphasis on ecosystem protection and less on timber production. Many wildland areas that are disturbed by major fire or harvesting activities—the situations that are the focus of this Guide—may return to a biologically diverse community with little to no intervention. However, the return of severely disturbed areas to a predominately native plant community within a desirable time frame can be unlikely, especially in areas with highly erosive soils or particular vulnerability to exotic invasive plant species. When recovery is problematic, seeding or planting seedlings can sometimes accelerate recovery, reduce erosion, or minimize invasion by exotic plant species. However, when the project objectives include ecosystem, restoration and biodiversity conservation, the decision to assist the regeneration of native plant species with seeding or planting involves risks: planting does not always improve recovery and has the potential to adversely affect biodiversity and sustainability of populations.

Some of the first questions following a disturbance such as a major fire or harvest are: What will happen if there is no intervention? Do we need to do anything to protect this area or adjacent lands, or to meet our objectives? For example, if there are concerns about soil erosion, aesthetic issues, or other considerations, the decision of whether to intervene will reflect that priority (see Box 5). There may be a certain urgency associated with the decision. For example, if a fire has removed exotic invasive species from a site, there is a limited window of opportunity to reclaim the site with native vegetation. There might be reasons to plant an exotic species, perhaps to improve site conditions for native species. There may be an interest in establishing a different successional (or seral) stage than the one that existed pre-disturbance. Those site-specific, social, economic, or political concerns will not be discussed here, nor will species selection—which can be guided by management goals and ecological considerations (see Boxes 6 and 7). The focus for this Chapter is the genetic considerations of natural regeneration versus artificial regeneration of native plant species. This focus assumes that one of the objectives for the project area is to re-establish native vegetation.

There are many different terms associated with the natural or assisted recovery of plant species following a disturbance. (See Harrington 1999, for example, for a discussion of the concepts associated with restoration, rehabilitation, and reclamation). The terms used in these situations often reflect three overlapping conditions: the management goal, the nature of the disturbance, and the steps taken (or not) in species recovery. To offer some objectivity to this discussion and to be clear about the focus of this Chapter, it is useful to briefly review the concepts associated with regeneration and define the terms used here.

Given the intent and scope of this Guide, it shall be assumed that the main or a major management objective is the restoration of native species and maintenance of biodiversity and healthy ecosystem function. Considering then the type of disturbance and the action taken by management, there are four possibilities for regeneration of native plant species:

1) The disturbance and the subsequent regeneration are natural;
2) The disturbance is natural, following by some assistance (such as planting);
3) The disturbance is human-influenced (for example, harvest or prescribed burn) but the regeneration is natural;
4) Both the disturbance and the regeneration are influenced by human activity.

Numbers 1 and 3 are often collapsed into the term “natural regeneration”; numbers 2 and 4, called “artificial regeneration” (Table 3.1). These terms are commonly associated with forest tree species, and may be less frequently used when other plant species are the focus. However, depending on the *nature* of the human-influenced disturbance, there may be more or less rationale for collapsing these four situations into two. For example, if a prescribed fire was the same in intensity, scale, and frequency as natural fires, and there was no planting or seeding after the fire, one could consider this a situation of natural regeneration by most definitions. Unassisted plant reproduction after a wildfire, or just gradually as recruitment possibilities occur, would also be natural regeneration. In these situations, numbers 1 and 3 (above), are basically identical. However, some disturbances might have impacts on the subsequent “natural regeneration”. For example, the regeneration of a forest tree species that results after a harvest that leaves seed trees might not be considered natural regeneration in the purest sense (although fitting a Forest Service definition). This is because the plants that germinated after harvest (from soil banks and canopy seed banks, from suckering, and from seeds blowing in) may differ in genetic composition from those that would have arisen through purely natural regeneration (no harvest activity) succession. And the harvesting activity may have affected subsequent reproduction of other plant species by soil compaction, changes in microsite conditions, and other impacts. Time can blur the genetic differences between types of regeneration. Depending on the nature of the seed or vegetative propagule sources, and site factors, the genetic diversity and structure of those species might eventually resemble (through continued reproduction and natural selection) that of “natural regeneration”.

For this discussion, the various definitions and understandings of the terms artificial and natural regeneration will be avoided by adopting the terms: “unassisted” and “assisted regeneration”. Unassisted regeneration simply means that no plants or seeds are intentionally introduced to the site to supplement recovery or regeneration of the native plant species. Assisted regeneration means that native plants are intentional introduced. Following a disturbance, there may be genetic consequences of either decision—providing (biological) assistance to the recovery or regeneration of the local native plant species, or not. By relaying some of the issues and context for each decision, it is hoped that the site manager may make a better-informed decision.

Genetic aspects of regeneration of plant species

The next generation of plants is never genetically identical to the current generation (Table 3.1). Even under completely natural conditions, the seedlings or sprouts are always just a sample of the genetic diversity in the parents. A certain amount of change from generation to generation is the natural, normal condition. Natural selection, in combination with other processes, acts to determine which plants survive and reproduce on that site over time. With vegetative reproduction of species, even though the sprouts are genetically identical to their parents, parents do not contribute equally to the next generation so there is a different genetic composition, and only rarely does a species exclusively reproduce by asexual means. And in the case of sexual reproduction, not only do the parents contribute to various (unequal) degrees, but their genetic diversity has been further mixed up or recombined in the progeny during meiosis. So the appropriate context for considering the genetic consequences of any kind of regeneration includes the fact that genetic diversity is dynamic and that the goal is not to exactly replicate the genetic diversity of the parental population. Rather, the goal is to have an adequate representation of the genetic diversity in the next generation to best respond to environmental changes.

Under conditions of unassisted regeneration there are various conditions that will influence the nature of the genetic diversity in the new generation of each plant species. These include:

- Whether the species reproduces only sexually or also asexually. Some plants, including some species of *Arctostaphylos, Ceanothus*, and *Mimulus*, can reproduce vegetatively by branch layering. Deeply buried corms, tubers, and rhizomes frequently survive fire and send up shoots in the first growing season after disturbance. As all individuals would not survive the disturbance, or respond with shoots to the same extent, the resulting genetic composition of plants would not be identical to the pre-disturbance situation.
- Whether there is a store of viable seeds in the soil or canopy (in the case of some tree species). Many species have seeds that lay dormant in the soil seed bank for years until environmental conditions trigger germination. Seeds of many species germinate in response to factors including various components of fire (heat, smoke, charate from the leaching of charred plant remains), mechanical abrasion of the seed coat (scarification), moisture, or to the increased light that occurs after the canopy is removed by fire or harvest (Fenner 1992; Young and Young 1992; Baskin and Baskin 1998a, b; Miller 2000). For some conifers, in particular, there may be a supply of viable seeds held in the canopy. In these cases, the cones remain attached to the tree and may contain viable seeds for many years. The scales on cones are tightly closed and open under hot dry conditions, including fire (called serotinous cones). The cones of Rocky Mountain lodgepole pine (*Pinus contorta* Douglas var. *latifolia* (Engelm.)), for example, can hold viable seeds for decades.
- Whether and how far seeds will travel to the site from neighboring plant populations. This varies greatly by species and depends on such factors as the size and shape of seeds, special adaptations for dispersal, and their mechanism of dispersal—by wind or carried by or attached to animals. For example, the tiny plumed seeds of fireweed (*Chamaerion*

angustifolium (L.) Scop.) are known to have dispersed more than a kilometer to isolated sites after the explosion of Mt. Saint Helen in Washington. The spores of bryophytes and ferns are especially light and buoyant and subject to wind dispersal. A review of seed dispersal in pine species concluded that species with seed weights less than approximately 90 mg are well adapted for wind dispersal; those with seed weights greater than 90 mg are poorly dispersed by wind and often have adaptations for animal dispersal (Benkman 1995). The seeds of whitebark pine (*Pinus albicaulis* Engelm.), for example, are dispersed, among other means, by the Clark's nutcracker (*Nucifraga Columbiana),* and may be carried over 20 km from the source tree and cached (Vander Wall and Balda 1977). Both Pinyon pine (*P. edulis* Engelm.) and limber pine (*Pinus flexilis* James) seeds are also dispersed by Clark's nutcracker (Lanner and Vander Wall 1980).

- Post-disturbance site conditions, including weather. Environmental conditions will help determine which seeds and seedlings survive and become genetic participants in subsequent generations of plants.

From these examples, it can be seen how the type of reproduction of a plant species and its seed dispersal mechanisms, in particular, have a large impact on the genetic diversity that results from natural regeneration.

Potential genetic impacts from unassisted regeneration following a disturbance

The type of disturbance (fire or harvest) and its particular nature (that is, type of harvesting system, characteristics of the fire) will have an impact on the amount and structure of genetic diversity left on site in the resident or adjacent germplasm sources (for example, Rajora and Pluhar 2002). In general, the regeneration will be affected by:

- The completeness of the removal of plant species (for example, a clearcut or intense, comprehensive fire versus selected harvested or a patchy fire, selective thinning with burning of slash piles)
- The damage to non-target plant species (in the case of harvesting) by mechanical disturbance, soil compaction, or other influences.
- The degree that the disturbance stimulates seed production, seed germination, or sprouting.
- Environmental conditions, including weather, that will contribute towards natural selection.
- Succession.

Much understanding about the effects of different forms of disturbance and regeneration can be gleaned from studies of commercially important tree species. Different harvesting methods leave different amounts and spatial arrangements of the target forest tree species on site and different levels of disturbance to non-targeted overstory and understory species. In diameter-limit cutting, most of the trees of a certain size are removed. However, depending on the availability of a persistent soil seed bank or canopy seed bank, and the number of juvenile trees, there could be sufficient genetic diversity left on site for natural regeneration to be a genetically appropriate option. With other harvest methods—such as seed tree or shelter wood harvests—the harvest is intended to leave sufficient reproductive material on site to make artificial regeneration unnecessary. However, even if there are adequate *numbers* of seedlings (or sprouts) from the trees left on site, they may be such a small sample of the original genetic diversity so as to narrow the genetic base of the forest population significantly. In addition, when the remaining plants are left in clusters, separated from each other by long distances, this could result in high levels of inbreeding if the plants in a cluster are closely related to one another. (In many species, neighboring individuals are often more closely related to one another than more distant plants and mating among close relatives often results in decreased survival fitness of the progeny. This "inbreeding depression" is a common phenomenon in many outcrossing species, especially tree species that normally produce most seeds through outcrossing. See Chapter 5 for more information on mating and inbreeding). The likelihood of adverse genetic consequences from natural regeneration following a harvest increases with a small or non-existent soil or canopy seedbank, few or scattered parent trees, breeding systems that are vulnerable to inbreeding depression, and site conditions that will quickly reduce the genetic diversity even further because of adverse regeneration conditions (Table 3.2).

The reported genetic effects of various harvesting methods on forest tree species are varied and inconsistent. In a comparison of genetic diversity in a mature (> 100 years) stand of lodgepole pine (*Pinus contorta* Douglas ssp. *latifolia* (Englemann) Critchfield) with a harvested stand left for natural regeneration, no significant differences in genetic diversity were observed (Thomas et al. 1999). However, in a more extensive study of the same species, harvest-origin stands were found to have significantly lower genetic diversity than unmanaged fire-origin stands (MacDonald et al. 2001). In the same study, no significant differences in genetic diversity were noted between regeneration methods on harvested sites (natural regeneration versus planting). These contrasting results with the same species illustrate how context-specific are genetic impacts.

A study of genetic diversity in eastern white pine (*Pinus strobus* L.) in Ontario, Canada, compared old-growth populations in pre- and post-harvest condition. In the natural regeneration following harvest, genetic diversity was lowered relative to the uncut stand—from 25% to 80% depending on which genetic diversity statistic was used (the mean number of alleles was reduced by 25%; percent polymorphic loci was reduced by 33%; 40% and 80% of low-frequency and rare alleles, respectively, were lost because of harvesting). This condition may mean that the postharvest naturally regeneration stand may have been compromised in its ability to adapt to changing environmental conditions (Buchert et al. 1997). Although the focus of the study was the commercial forest tree species, other plant species may have been similarly affected in their genetic diversity.

Another study compared genetic diversity in Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*) in unharvested stands with regeneration in adjacent stands harvested at various stages: the trees left in shelterwoods, seeds from those trees, and 3-5 year-old seedlings from those seeds. The authors did not find any significant genetic differences in comparing these four groups. However, they emphasized that the absence of genetic differences may be because of species characteristics (for example, Douglas-fir has considerable genetic diversity within its populations and high out-crossing rates) (Neale 1985). A similar comparison with another plant species with contrasting characteristics might show different results.

Differing results from such studies that compare genetic impacts of various harvesting methods and fire disturbance with natural regeneration should not be surprising. First, as mentioned earlier, fires and harvests can be vastly different in impact (intensity, coverage) and thus have different genetic impacts. Second, different species would be expected to respond differently depending on whether or not there was a soil or canopy seed bank, their breeding system, whether they are monoecious or dioecious, and whether they also reproduce vegetatively. Third, the conditions on neighboring sites would have an impact on natural regeneration on the target site. Fourth, specific site conditions will greatly influence the degree to which remaining plants or seeds can contribute to the next generation. Soil disturbance—including changes in drainage, soil compaction, changes in soil structure and piling of soil and woody debris—influence which seeds or seedlings are better adapted to the site conditions and thus affect the resulting genetic diversity on the site. Weather conditions, in particular, will affect which seed or seedlings are recruited into the next plant population. And finally, the 'control' or the natural site with which the disturbed site is being compared (and thus, by which the impacts on genetic diversity are being measured) can vary in its resemblance to a natural forest. Even if the "natural" forest area has not been harvested, there could be influences on its genetic diversity such as those from thinning, introduced diseases, and pollination from planted trees in adjacent sites.

The disturbance may also affect the natural seed (or pollen) dispersal mechanisms. For example, species with bird-dispersed seeds may experience less seed dispersal as a result of the disturbance. There could be several reasons for this. First, birds may avoid the open areas surrounding the few remaining seed trees as they are more vulnerable to predators in such conditions. Secondly, if more plentiful food sources are available elsewhere, the fruit offered by the few remaining and isolated plants may not be sufficiently attractive. An example of a species whose reproduction would be impacted by removal or scarcity of pollinators is the perennial herb, *Ipomopsis aggregata* ((Pursh) V. Grant) found throughout montane western North America, including Wyoming and Colorado. The primary pollinators for this species in its western Colorado populations are the broad-tailed (*Selasphorus platycerus* Swainson) and rufous (S. *rufus* Gmelin) hummingbirds (Waser 1978). A well-studied species, it has been estimated that only about 1% of its ovules set seed if pollinators are excluded (Waser and Price 1991). Finally, if a plant species relies on insect or bird pollinators, but is also capable of vegetative reproduction, the scarcity of pollinators might shift the plant towards more vegetative reproduction, at least in the short term.

In general, the more complete the removal (or severe the disturbance) of parent material and seeds, the more likely the need for assisted regeneration. However, a countervailing influence for some plant species is that the disturbance may stimulate production of new plants. Both fire and harvesting stimulate sucker development in some species, such as quaking (or trembling) aspen (*Populus tremuloides* Michx.) (Frey et al. 2003). Nevertheless, other harvest-related conditions—including skid trails, landings, and retention of slash—generally reduce sucker initiation and growth (Frey et al. 2003). For species that are facultatively clonal (meaning that, in addition to producing seeds, they can reproduce by vegetative means) and tend to be dominated by few, old, clones with many stems, a fire or harvest followed by natural regeneration may be an opportunity to get rid of old dominant clones that are not well-adapted to current, and probably future, environments. For example, the extreme longevity of quaking aspen suggests that extant stands in some areas are comprised of individuals which may no longer be adapted to current conditions (Stevens et al. 1999). However, the genetic aspects of natural regeneration of an asexually reproducing species may be complicated, even within the same species. Quaking aspen is North America's most widely distributed native tree species, and its genetic patterns related to reproductive behavior may vary considerably from region to region. Furthermore, in some cases, different members of the same clone may have different genetic compositions, the apparent result of somatic mutation (Wyman et al. 2003). Thus, for this species at least, vegetative reproduction—at least over the life-span of individual trees—is not synonymous with genetic replication.

Potential genetic impacts from assisted regeneration following a disturbance

Following an intense and far-reaching fire, it may be natural to assume that some kind of intervention is required to establish native vegetation on the site. However, this decision should be well-considered: there are consequences and (perhaps unnecessary) expenses from immediately discounting natural regeneration (Table 3.2). The legal requirement, however, for adequate regeneration to be achieved within a five-year window, even for salvage sales, imposes some restrictions on the ability to allow natural regeneration to achieve management objectives.

Introducing plant material to a site presents risk that ranges from minimal to severe. These risks are explored in more detailed elsewhere (Chapters 1 and 7). In brief, if material is not locally adapted, or is collected from a narrow genetic base, the regeneration that follows may not survive—either in the short term or long term; however, the risk does not end with proper selection of genetic material. Even if the genetic source is properly selected, there can be genetic impacts from the way the seeds or other plant materials are germinated, raised, or otherwise managed. For example, if the plants are raised or the seeds multiplied in a nursery setting, there could be genetic impacts from that environment—which is usually dissimilar in some respects from the conditions at the final planting site (Campbell and Sorensen 1984, Kitzmiller 1990, and Chapter 8). Those impacts could mean that less genetic diversity arrives on site than was represented in the original sample or that the seeds or plants have been selected for a nursery environment rather than the restoration site conditions.

Planting seedlings or cuttings, or even broadcasting seeds, to some extent, also carry some risk of inadvertently introducing undesirable genetic material in the form of exotic invasive plant species or pathogens. These could be carried in the soil of containerized material, an undetected element of a seed mix, or harbored in straw or duff used as mulch around new plantings to stabilize a site.

Nevertheless, there are species and situations where genetic intervention may be required if the disturbance area is large and unlikely to receive dispersing seed from neighboring unburned areas. Nuttall’s larkspur (*Delphinium nuttallianum* Pritzel) is one species that might require reintroduction on some sites, following particularly high intensity catastrophic fires. It is a small herbaceous perennial plant that does not reproduce vegetatively and there is virtually no soil seed bank beyond one year. Furthermore, reproductive maturity is not usually reached until the plants are 3-7 years old (Williams and Waser 1999).

In summary, if site conditions are favorable, natural regeneration may be the best option for protecting genetic integrity and maintaining local adaptation of the local plant species. If there aren’t other serious considerations, if there is reasonable likelihood of resprouting or a local seedbank or seed rain from adjacent areas, then natural regeneration may be the most genetically appropriate option. Local seed sources (assuming the original plants on site prior to disturbance were local) are usually preferred to meet land management objectives on National Forest System lands and natural regeneration rules out the possible negative impacts from ill-matched seed sources, nursery impacts on genetic diversity, or inadvertently transporting exotic insects or pathogens to the site with planting materials.

Managing plant species for climate change

As a final topic in the discussion of genetic impacts of assisting or allowing natural regeneration, the issue of climate change is relevant. Should there be aggressive management in anticipation of some major shifts in species' ranges and best-adapted genotypes? Will natural selection be sufficient to maintain species viability with the accelerated rate of climate change? Indications are that climate change is occurring at an accelerated rate. Temperatures rose in the 20th century at a rate unprecedented in the last millennium. Atmospheric CO_2 concentration is now higher than at any time in at least the last 420,000 years and will almost certainly double within the next century (Bradley 2000). Changes in the normal range of temperatures, patterns of precipitation, concentration of CO_2, and other atmospheric characteristics affected by recent and continuing climate change, will affect forest dynamics and possibly species' ranges (Peters 1990). Globally, these effects are expected to be more pronounced in temperate (including Region 2) and arctic forests, where temperature increases are projected to be relatively large.

Historically (that is, evolutionary time-scales) plant species adjusted to changes in climate by migrating to new conditions, changing their natural range over time. This migration requires that there be available habitat in close proximity to existing habitat, allowing natural regeneration to gradually shift into more desirable areas. Depending on site conditions, some species may no longer have sufficient migration options, being hemmed in by development, agriculture, or other land uses. Species may also be able to adapt to new climatic regimes in their current ranges if they possess sufficient genetic diversity. Many species can also accommodate considerable impact of climate change through variation in their phenotype (various traits) rather than actual genetic changes. But the latter mechanism has limitations.

Some species may be able to respond fairly quickly to climate change. In particular, species that have considerable amounts of genetic diversity and short generations have the basis for rapid adaptation. For example, a genetic shift in photoperiodic response (correlated with global warming) has already been observed in an insect, the pitcher-plant mosquito (*Wyeomyia smithii*). This mosquito relies on the purple pitcher plant (*Sarracenia purpurea* L.) during its pre-adult development and therefore is highly coincident with the plant's range, occurring over a wide geographic area in eastern North America. By subjecting the mosquito to different climatic conditions in controlled environment chambers, genetic responses could be measured. The shift in genetic variation in response to changing environmental conditions was detectable in as little as five years. Faster evolutionary response has occurred in the northern populations of this mosquito, presumably because of the greater amount of genetic variation (relative to southern populations) and the strong selection pressures there (Bradshaw and Holzapfel 2001).

Because of their longer reproductive cycles and lifetimes, this approach to measuring adaptive responses to climate change in long-lived plant species is less practical. One approach has been to measure both plant growth characteristics and climate in a number of common garden studies that contain multiple populations of a widespread species, and then develop models that relate climate to growth. Such studies for lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) demonstrated that the natural populations have different climatic optima and that the same processes thought to determine the distribution of species control the distribution of genotypes within species. Furthermore, the results of this study suggested that even small changes in climate will greatly affect growth and survival of forest tree populations (Rehfeldt et al. 1999).

Although a thorough review of this topic and specific recommendations are beyond the scope of this Guide, a few general points to consider in managing plant genetic resources in the presence of accelerated climate change include:

- Allow opportunities for plant populations to respond to climate change through migration at least in some directions, by avoiding the creation of hard edges (in all directions) with inhospitable land uses such as concentrated housing developments, airports, intensive agriculture, and other such uses.
- Maintain genetic variation within populations to allow as much adaptation in place as possible.
- Consider shifts in population and species ranges when developing seed procurement plans. Even if the effects are longer term than a 10-year management interval, any management responses to long term environmental changes will still need to be gradually accommodated through shorter term plans.

Table 3.1. A classification for plant growth following a disturbance.

Disturbance	**Regeneration**	**Common description**	**Genetic effects (relative to pre-disturbance)**	**Description used in this Guide**
Natural (such as natural fire)	Natural (such as germination from a seed bank or sprouting from roots)	Natural regeneration	Potentially small, but plants are still genetically different from previous vegetation	Natural regeneration
Natural	Assisted (such as planting or seeding)	Artificial regeneration	Range: small to potentially large	Assisted regeneration
Human-influenced (such as harvesting)	Natural	Natural regeneration	Depends on the type of disturbance, the species, and environmental factors	Natural regeneration
Human-influenced	Assisted	Artificial regeneration	Range: small to potentially large	Assisted regeneration

Table 3.2. Risks and opportunities associated with natural (or unassisted) regeneration and assisted regeneration of native plant species on sites where fires or harvests have occurred. (See text for definitions of terms.)

Type of regeneration	**Types of associated risks**
Natural or unassisted regeneration (no planting or seeding)	-Residual plants or seeds may be too two or sparse and genetic diversity may be lowered. -Severely unequal sex ratio (for dioecious plants) may exist, reducing genetic diversity in progeny. -Too few residual parent plants may lead to inbreeding depression in some species. -Residual plants may be too sparse or isolated to attract pollinators or seed dispersers in plant species that have such associations. -Original plants may not have been local (for example, this could have been a plantation that had been established with plant materials from a distant population that differed genetically from local populations).
Assisted regeneration (planting or seeding)	-Introduced plants or seeds may not be adapted to site (and thus, may have poor survival or exhibit other expressions of maladaptation). -Introduced plants or seeds may come from a narrow genetic base (for example, one family, cultivar, or clone) and thus lower genetic diversity relative to original population. -Additional, and undesirable, genetic material may arrive unintentionally onsite with the plants (for example, weed seeds or pathogens in the soil of containerized material).

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Box 5: The Recurring Question: To Seed or Not to Seed?

After a large wildfire, news headlines will often state in large bold print "Wildfire! Many thousands of acres of hilly shrubland and forest burned!" Such a headline could be for Arizona, California, Colorado, or any of a dozen states, all within the last few years. The article likely explains that dozens to thousands of structures in the wildland-urban interface burned to the ground and tragically, lives of a dozen residents and fire fighters were lost. The fire has removed the protective cover of vegetation, exposing soil and debris to the erosive forces of wind, rain, and gravity. First, there is dry ravel, the down slope movement of loose soil and rock materials under influence of gravity, and freeze-thaw processes. Then, there is water and wind erosion of unstable soil and debris. The combination can pose a serious threat to down slope structures and resources. Water companies, local residents, and business owners become uneasy about the debris flows that could spill down the slopes, corrupt drinking water supplies, and damage aquatic habitat. Residents and land managers are especially concerned about the potential for life-threatening mudflows following the next heavy rain or snow melt. Burned Area Emergency Response (BAER**)** teams congregate to analyze erosion hot spots and to designate emergency erosion control strategies needed to save lives and property.

The public has heard for years that seeds must be broadcast on slopes to replace the lost vegetation because roots bind soil, aid in percolation of water, and lower runoff potential. There is public pressure for land management agencies to seed burned slopes with fast-growing species, especially steep slopes by major watercourses or near developments. Furthermore, agencies are expected to move *quickly*. However, every burn site has its own context and host of questions:

- What is the evidence and probability that emergency seeding will produce plants capable of reducing the impending erosion in this critical first season for the type of burn site?
- Will seeds actually stick to the slope, germinate, and grow before a storm washes seeds, ash, and unstable soil downhill?
- Is there a deficit of viable seeds in the soil, or existing live roots, rhizomes, and other storage organs of perennial plants? Are there perennial species that resprout quickly after fire and seeds of annuals and perennials that germinate in response to fire?
- Under what conditions is natural regeneration so sparse that seeding is worthwhile?
- Is seeding with non-native species, non-local native accessions, or native cultivars likely to be beneficial or harmful to the native community? What are the relative prices?
- Will invasive species invade the newly exposed sites and gain a foothold before native plants can reestablish if a "nurse crop" of native or exotic non-invasive grasses isn't planted?
- Are there any ecologically and genetically appropriate native seeds available?
- Are there exotic grasses that can be used as an alternative to local natives and if so, are they invasive or non-persistent? Do they interfere with recovery and establishment of native plants? Is there enough information available for an environmental assessment?
- How should a lower budgetary cost be balanced against the potential environmental cost?

Many of these questions can't be answered quickly. Others may have little science on which to base responses. Still others may have been investigated but the results may contradict ingrained management practices, making the response politically difficult to defend. Decisions about BAER seeding must be based on the present situation together with careful evaluation of past research and monitoring results rather than anecdotal evidence.

Robichaud, Beyers, and Neary (2000) reviewed three decades of data on the usefulness of postfire seeding. Unfortunately, those data did not tell a clear story of beneficial reductions in erosion. As might be expected, results varied with site, rainfall, and seeded species. Forested areas were more likely than dense shrubland (chaparral) to benefit from seeding. In many situations, seeding with exotic plants, especially grasses, had little or no significant erosion control value. Instead, if the seeds hadn't washed down slope with the first heavy rain, the non-native plants interfered with natural regeneration of native plant communities. Seeded plants frequently did not lessen erosion until after the most dramatic erosion-causing storm events. In a recent study that examined sediment movement after hydroseeding versus aerial seeding, only the hydroseed treatment that contained wood fiber reduced sediment loads (Dyer et al. 2003).

Seeding with exotics, if it doesn't prevent erosion, may simply conflict with the Forest Service mission (Box 3, Chapter 2). Federal Acts and Executive Orders authorize and direct the Forest Service to maintain biodiversity and protect natural resources in a multi-use context (Box 4, Chapter 2). Consequently, Forest Service Districts and National Parks in Colorado, Wyoming, California, and other western states are opting for less seeding and more mechanical erosion control treatments (BAER 2003, Robichaud et al. 2003, Turner et al. 2003). Some non-profit groups also recommend mechanical methods, natural plant recovery, and avoidance of seeding after wildfire (CNPS 1995).

In some areas, seeding is thought to be effective. In Montana, the USDA Natural Resource Conservation Service Plant Materials Program recommended seeding of 6,000 acres after a 2001 wildfire. The decision was based in part on a 30-year study in Montana that found significant increases in vegetative cover after seeding in certain habitats after fire (Hunter 2003). There was less advantage to seeding postharvest. The study also found a reduction in tree seedling numbers in some seeded areas. The study did not measure erosion directly; it assumed an increase in vegetative cover equated with decreased sediment flow. Montana has a variety of native plant materials available for seeding. The question remains—what amount of cover is sufficient to make a difference in sediment flows, or lessen invasive species takeover, and is the seeding cost effective?

When seeding is prescribed, there erupts a flurry of questions about the availability, costs, benefits, and risks of using genetically-local native seeds, translocated-native seeds, selected native cultivars, or exotic grasses. The Forest Service Handbook (Title 2400 for trees and shrubs in Region 2), and the Forest Service Manual (Titles 2500 and 4000 Service-wide for all plants), taken together, make use of genetically-local plant materials over non-local natives and non-persistent exotics a priority (Box 3, Chapter 2). However, resources must be found quickly and there is little time to make decisions about what seeds to use. Because prices are sometimes lower, and availability higher, some agencies provide information for use of persistent (sometimes invasive) exotic species, non-persistent exotics, and non-local native-plant releases (see more about native plant releases in Chapter 8). Such recommendations sometimes lack supporting information about potentially beneficial or adverse effects on native plant communities (for example, USDA NRCS 2003). The use of non-local natives is sometimes nearly as controversial as the use of exotic species (Box 6). In contrast, some non-profit seed networks help to coordinate seed growers, sellers, and seed buyers so that the most genetically appropriate seeds are available at a reasonable price (for example, Native Seed Network 2004).

There continues to be considerable discussion, debate, and study about when and if seeding treatments are effective (Barro and Conard 1987, Keeley 1994, Wohlgemuth et al. 1998, Paysen et al. 2000, Robichaud et al. 2000, Turner et al. 2003, Keeley 2004). Some of the debates and difficulties behind decision-making make the news (L.A. Times in Keeley et al. 1995, Matthews 1997). In the meantime, the Forest Service keeps the public well informed about reasons for BAER decisions through press releases and electronic posting of BAER reports (BAER 2003, USDA Forest Service 2003). The Forest Service shoulders a careful balance of conservation interests and protection of life and property.

The Forest Service and other agencies have produced many publications that help to determine if seeding after fire is necessary. See Robichaux et al. (2000) for details of BAER history and challenges and an extensive review of postfire treatments. A detailed chapter on fire autecology in the USDA Forest Service “Rainbow Series” provides an overview of the many mechanisms by which plants resprout and colonize naturally after fire (Miller 2000). Miller also describes the kinds of traits associated with surviving fire and the effects of fire intensity on survival and resprouting potential. Another resource for information about the fire ecology of about 900 plant species, including many invasive species, is the “Fire Effects Information System” internet database (FEIS 2004). The database is easy to use and it provides information about the taxonomy, habitats, and fire ecology of trees, shrubs, grasses and forbs. Dyer (1995) reviews quick methods for determining seed bank quality after fire. Korb et al. (2004) show how more intense fire can deplete seed banks and open up sites for invasion. Another very interesting area of research examines how invasive non-native species, sometime previously seeded, affect fire cycles and restoration of pre-invasion fire regimes (Brooks et al. 2004). Finally, Brown and Amacher (1999) suggests there are many myths needing evaluation regarding the environmental and fiscal costs of using non-native species compared to native species in land rehabilitation.

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Box 6: Ecological Genetic Considerations in Species Selection.

Species selection is the critical first step in guiding choices about what genetic material to use. It is critical to natural biodiversity and potential success of all kinds of planting projects, whether for agricultural projects, landscaping, or ecological restoration. For restoration, the choice of species is guided by numerous factors. With the exception of a temporary nurse crop, of foremost importance is selection of species that are adapted to the specific habitat that will be planted, not just to the local region. For restoration, this includes correct assignment of subspecific taxa. Many closely related species and their subspecific taxa are difficult to distinguish, but often they are adapted to different conditions and represent different ecotypes. There may be some situations where slight range extensions of taxa are appropriate. Researchers have been exploring potential effects of rapid climate change, habitat fragmentation, and destruction of dispersal corridors on persistence of populations and species. However, plants track their environments in complex ways that can't always be anticipated. There is an interest in understanding when range extensions can occur without adverse consequences. More generally, it is important to match the correct local taxon to its environment, to consider carefully the successional status of a species in relation to current site conditions, and to maintain possible dispersal corridors.

This box provides a brief introduction to some of the problems associated with inappropriate species choices. It is important to consider potential, and possibly far reaching unintended consequences of introducing new species to a site. The concepts provided should be considered when adjusting species lists. A related box (Box 7: Some Ecological Resources Available for Guiding Species Selection) provides a few references to aid initial choices.

Lack of appropriate adaptation. Placing plant species in the wrong environment is a major cause of planting failures. The wrong taxon may not be able to grow vigorously, survive or reproduce. As indicated in Chapter 7, it is sometimes difficult to separate failures due to translocation of inappropriate genotypes within a species with simply mismatching a species to a site. There are many examples of restoration and postfire rehabilitation for which species or subspecies native to the same continent but not to the project site have been specified or used for planting (discussed by Monsen 1975, Mulroy 1990, Keeley 1998). For example, there are many restoration projects in southern California that planted taxa that were not native to the location. For example, *Encelia farinosa* Gray ex Torr. of inland habitats has often been seeded along the coast where the closely related *E. californica* Nutt. is native (and *vise versa*). *Baccharis pilularis* DC, from upland habitats has been planted instead of *B. emoryi* Gray in riparian habitats. The varieties of *Lotus scoparius* (Nutt.) Ottley and *Eriogonum fasiculatum* Benth. from moist coastal locations have often been planted at dry inland sites (A. Montalvo, personal observation).

Why do such mismatches occur? First, there may be accidents caused by lack of specifying precise subspecific taxa followed by using materials translocated from a different habitat or region. Many subspecific taxa are associated with different habitats (e.g., Meyer and Monsen 1990) so this can result in differently adapted taxa planted at a site. Second is purposeful substitution with similar species meant to satisfy particular ecosystem functions because they happen to be commercially available or cost less then local taxa. This may happen when insufficient time or funding is available for project planning and plant procurement, such as after emergencies. Third is transcription error in record keeping or labeling at the level of seed collection, processing, and production. Forth, is error in plant identification. Use of resources collected within the same region and habitat type, salvage of seed banks, encouraging natural regeneration, custom seed collection and production, or use of certified plant materials can eliminate most problems (Mulroy 1990, Meyer and Monsen 1993).

New invasions. Many species are perfectly capable of growing and reproducing in areas far from their native homes in regions that have very similar physical environments, or if the species is broadly adapted. In fact, many of the most vigorous invasive species have jumped continents with the aid of humans and invaded sites in climatic regions similar to their original homes. For example many species of Mediterranean grasses have invaded much of California, and some species from California, including the Sate wildflower, the California poppy (*Eschscholzia californica* Cham.), have invaded similar climate regions in Chile and Australia. Invasions can also involve species that have crossed former ecological or geographic barriers within continents with the aid of humans, and still others involve very distant translocations of a single species that has a range spanning multiple continents. With much assistance by humans, California poppy has also invaded sites within its home continent outside its native range. There have been range extensions of numerous other plant species, followed by a newly acquired "weediness" if not already a "weedy" colonizer within its native range (Baker 1995). Baker described the expansion of the pineapple weed, *Matricaria discoidea* DC. (cited as *Matricaria matricarioides*). This self-pollinating, colonizer is native to the northwestern North America, but rapidly spread all over North America, Europe, and northern Asia. Such range extensions can be problematic if the new populations become highly aggressive. Sometimes there is a long lag period before a human-mediated introduction crosses the threshold from a colonizer, to aggressive competitor, to invasive organism. In the case of cordgrass (*Spartina alterniflora*) introduced to Willapa Bay, WA in the 1890s from eastern North America, the plant covered about 400 acres by 1982. Then, 22 years later, over 6000 hectares of tidal flats were covered. Such lag periods followed by rapid expansion and invasion can result from evolution and adaptation, global warming causing a shift in conditions more suitable to the plant, or having reached some critical density needed for successful pollination (Parker 2004).

Hybridization between native and introduced species. Many examples of hybridization between native and introduced species or between two introduced species can be found in Ellstrand and Schierenbeck (2000) and Ellstrand (2003). Although some hybridizations result in long-term benefits, some highly damaging situations have erupted from introduction of species that hybridize with resident species. In addition to outbreeding depression (Chapter 5), there can be the evolution of new invasive taxa or genetic swamping (genetic assimilation) of resident species. Genetic assimilation of rare species by introduced species can be mediated by directional gene flow into the resident population, followed by backcrossing to the introduced taxon. When the hybrids and introduced taxon are superior competitors, there can be local extinction of sensitive populations (for examples and models see Rieseberg 1991, 1995; Rhymer and Simberloff 1996; Huxel 1999, Storfer 1999, Wolf et al. 2001).

Perhaps the most notorious and best documented examples of introduction, hybridization, invasion, and local extinction (also called extirpation) involve the grass, *Spartina alterniflora* Loisel., which is native to salt marshes along the coastal, eastern US. Many years ago, we learned a difficult lesson after this species was introduced to salt marshes in Europe where it hybridized with the native resident *S. maritima* (M.A. Curtis) Fern. (Baker 1995). This resulted in the emergence of a new hybrid, *S.* x *townsendii*, which at first expanded by vegetative means. The hybrid then underwent a doubling of chromosomes and formed a tetraploid derivative species, *S. anglica*, which regained fertility and became even more invasive than its introduced diploid progenitor. But the lesson didn't stop there. *S. alterniflora* and three other invasive species of *Spartina*, including the new hybrid species, were then introduced to the west coast of North America. Three were brought in for restoration work. *S. alterniflora* subsequently hybridized with the resident native *S. foliosa* Trin. and produced an enormously aggressive hybrid that has been genetically swamping and out-competing populations of the native *S. foliosa*, causing local extinctions. Swamping of the resident populations was aided by vegetative reproduction and the much higher pollen production and siring of seeds by individuals of the introduced species. The hybrid has rapidly spread and filled in large portions of bays and estuaries around San Francisco causing much damage to the saltmarsh ecosystem and the utility of the bay for navigation. The progress of the new invasive hybrid has been tracked and studied in detail using molecular markers (Ayres et al. 1999, Daehler et al. 1999). A website is devoted to the *Spartina* invasions (http://www.spartina.org).

Identification errors. An interesting example of an error in identification that lead to unintended consequences is the story of the plant materials release 'Appar' described by Kitchen (1995, 2002). The North American species of Lewis flax (*Linum lewisii* Pursh) is morphologically very similar to, but reproductively isolated from the blue flax of Eurasia (*Linum perenne* L.) which has been extensively planted in the US. 'Appar' was developed and selected for broad tolerance and released as a selection of the native Lewis flax in 1980. Unfortunately, it was selected from an accession of naturalized blue flax from North Dakota, which the collector had incorrectly identified as the native *L. lewisii*. The release was used inadvertently in place of *L. lewisii* in wildland and roadside plantings for over a decade until it was discovered that it was indeed the Eurasion species, *L. perenne*. Kitchen (2001) found that 'Appar' and Lewis flax have distinctive adaptive differences in seed dormancy and chilling effects on germination. The non-dormant seeded 'Appar' is not expected to reproduce successfully in many areas where seed dormancy is important to survival of Lewis flax. However, some of the 'Appar' plantings were found to be so vigorous that the Colorado Weed Management Association (CWMA) placed blue flax (then called *L. lewisii* var. *perenne*) on the list of "invasive ornamentals" in the CWMA handbook "Troublesome Weeds of the Rocky Mountain West" (Kitchen 2002). Seed industry and plant materials specialists concluded there was a lack of evidence to support this designation and the plant was dropped from the list.

Disruption of species interactions. Natural communities are composed of many interacting species, both above and below ground. Many species interact with many other species (as when a particular food plant is utilized by many species of herbivores and serviced by many species of pollinators). Other, more specialized interactions involve few species, and many are species-specific. The one-on-one interactions can be critical to survival or reproduction and are particularly vulnerable if other species are introduced. For example, the success of butterflies depends on the timing of egg hatching and relative to the stage of growth of their host plants. Both plant and insect activity may be conditioned to respond to similar environmental cues (Pratt 1994, Pratt and Balmer 1991, 1993, Longcore et al 2000). When planting projects aim to manage biodiversity, it is important to consider the many interactions among species, including microorganisms, fungi, plants, invertebrates, and vertebrates.

The case of the rare El Segundo blue butterfly (Longcore et al. 2000) illustrates how planting the wrong species can be problematic. California buckwheat (*Eriogonum fasciculatum*) has wide geographic variation, is a host for many insect species, and is commonly used in restoration projects throughout the Southwest, even in areas where the plant does not occur naturally. This common buckwheat was used in a dune restoration project in coastal San Pedro, CA where a completely different species of buckwheat, *E. parvifolium* Sm. in Rees, was the native resident. The rare El Segundo blue butterfly feeds only on the late blooming flower heads of the resident species. At the site, a diversity of competing insect larvae fed on the earlier blooming *E. fasciculatum,* built up their populations, then also fed on the later blooming native *E. parvifolium*. This resulted in a doubling of insect populations that competed with and depressed the rare butterfly population. Evidence for the coordinated evolution of plants and the organisms with which they interact is discussed in Thompson (1999) and Calsbeek et al. (2003).

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Box 7: Some Ecological Resources Available for Guiding Species Selection

The information provided in the body of this guide assumes that a working list of species for a planting project has already been put together. The *initial* selection process is primarily guided by *ecological* rather than *genetic* concerns and is not a focus of this guide. Box 6 (Ecological Genetic Considerations in Species Selection) provides some concepts to consider in revising a species list due to potential ecological genetic consequences on the populations being restored. As pointed out in Box 6, it is important to choose species, subspecies, and varieties that are adapted to the specific habitat that will be planted, not just to the local region. Most people will rely on their own local knowledge of an area for making initial species selections, but some useful tools can augment personal experience. This current box provides a few references for aiding the initial ecological step in the selection of species. Some of these tools can also be useful when deciding on the appropriateness of moving populations around within their home ranges. This is by no means a comprehensive list.

When choosing species for restoration, projects will assume less risk and will most successfully facilitate native biodiversity and ecosystem integrity if the plant species list is carefully assembled and taxa are correctly assigned to native habitats. There are several techniques and published guides available to help select native species for revegetation projects. First is choosing an appropriate reference site and learning about the species that occur naturally during different successional stages. The SER Primer on Ecological Restoration (Society for Ecological Restoration 2002) provides information about use of reference sites that is valuable to all geographic regions. Other guides are available that can augment the use of reference sites. Within Region 2, the Native Plant Revegetation Guide for Colorado (Colorado Natural Areas Program 1998) describes the floristic regions of Colorado, provides detailed plant community descriptions and plant lists, in addition to community dominants, for each plant community. The three volume Restoring Western Ranges and Wildlands (Monsen et al. 2004) contains ample information on the ecology and restoration techniques useful in taxon selection and planting for many species native to Region 2.

New methods to assist with choice of plant species are under development. Computer technology and a geographic information system (GIS) allow users to assess lists of plant species that are both ecologically appropriate for the planting site and potentially useful for controlling erosion on denuded roadcuts and roadsides (Curto et al. 2002). GIS overlays provide hydrologic units of classification with links to physiographic and climatological data. This is used together with information about the presence or absence of a selected plant species. The GIS uses a California “Plantclimates” map which has been refined to include elevation contours and topography. The Plantclimates are similar in detail to the finest divisions of Level IV Ecological Units subsection maps produced by the US Forest Service (Goudey and Smith 1994). Many other overlays aid in location of potential reference sites. Though not as detailed as the above model, GIS information on herbarium collections for at least Wyoming and Colorado is available online through the Atlas of the Vascular Flora of Wyoming mapping project (Rocky Mountain Herbarium 2004). Many herbaria have been working to make their collection data available online. Such systems can also be used, for example, to identify locations of populations relative to project sites.

Other maps are available that can be used in combination with detailed plant lists. These include, for example, Küchler’s Potential Natural Vegetation Maps (Küchler 1970, 1977, 1985), Level 4 Ecoregion Maps (scale 1:1,000,000, see below), and Soil Conservation Service Major Land Resource Areas with evapotranspiration zones (US Geographic Survey 1985). An example of a less detailed resource than the two previous examples focuses on revegetation of roadsides, but it covers all regions within the US. For each state, Harper-Lore and Wilson (2000) provide the Küchler maps with a key to major plant associations. They also provide a list of native species to consider for roadside revegetation with added citations to local floras and people that can assist with details. The lists do not cross-reference the particular plant association or different habitats, and so are of limited use for accurate habitat matching. In addition to on-the-ground- studies, the online version of the Flora of North America (Flora of North America Editorial Committee 1993+) Plants Database, and FEIS (2004) can be used to help research distributions and habitat affinities for individual taxa.

The Native Seed Network website has a page that describes the different kinds of ecoregion maps, explains the data that were used to prepare each type of map, and provides links and references for obtaining them (Native Seed Network 2004). Level IV maps are the most detailed and can be used to help match species to general locations (but not necessarily to particular habitats within). The following maps and links are provided at their site.

- EPA (Omernik's) Ecoregions: Level III Ecoregion map for the US can be downloaded from the EPA website (http://www.epa.gov/bioindicators/html/usecoregions.html). The site also provides a link to Bailey's ecoregion maps and provides more information about development of the maps. For example, view map for North and South Dakota: http://www.npwrc.usgs.gov/resource/1998/ndsdeco/ndsdeco.htm.
- USDA Forest Service (Bailey's) Ecoregions: Ecoregion information page: http://www.fs.fed.us/institute/ecolink.html Map at: http://www.fs.fed.us/institute/ ecoregions/na_map.html
- MLRA (NRCS's) Ecoregions: Major Land Resource Areas map at: http://www.nrcs.usda.gov/technical/land/mlra/
- GIS (spatial files, Geographic Information Systems) can be downloaded from: http://water.usgs.gov/lookup/getspatial?mlra

Another useful map: USDA Plant Hardiness Zones available at the United States National Arboretum site: http://www.usna.usda.gov/Hardzone/ushzmap.html.

Workshops are held every year by various agencies and groups with experts to assist land managers with issues of species selection. It helps to keep informed about those in your area.

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Chapter 4

Description of Genetic Diversity

The nature of an individual—whether plant or animal—is influenced by its genetic code (its DNA), its environment, and random events during development. The particular environment experienced by an individual can influence how that individual looks and functions. Because every individual is genetically unique (with the exception of clonal replicates), and because there are infinite variations on the environment experienced by each individual, this results in a large array of variation in plants and animals within a species. The term “genotype” refers to the specific genetic constitution of an individual. Because the environment experienced by any genotype has a great deal of influence on its functioning and appearance, it is useful to separate genetic and environmental effects (this reflects the “nature versus nurture” discussion for humans). The “phenotype” is the resulting appearance, physiological condition, or behavior that results from the combined influence of the DNA and the environment. So, phenotype is what we see—a plant’s size, color, seed yield, for example, as well as other kinds of functional attributes that can be measured, such as photosynthetic rate, how long it takes to reach flowering size, or the sweetness of a fruit.

This relationship of environment and genotype to produce individual traits has been represented by a simple expression: P (phenotype) = G (genotype) + E (environment). From this simple expression, a mathematical model has been constructed that takes into consideration the total variation among phenotypes within a collection of related individuals, that is, within a population. Then it is possible to determine how much of the variation in a trait is caused by differences in genetic composition versus the influence of the environment. Other terms can be added to the model, such as a term for an interaction between G and E (G x E). It can be seen from this simple model that different phenotypes will develop if you change either E or G, that the same phenotype can arise from various combinations of E and G, and that the same genotype (for example, a clone) can look different if grown in different environments.

In much of this practical guide, we focus on the “G” component of this relationship. As will be seen later, we also focus on the interaction of G and E because that relationship forms the basis of local adaptation. In this chapter, we consider the amount and kind of genetic variation within species, how it is organized, what measures we use to describe it, and the natural processes that influence it. By reviewing the concepts that underlie genetic diversity, including its pattern, we pave the way for understanding the ecological and evolutionary context of genetic diversity (Chapter 5), the nature of local adaptation (Chapter 6), and the consequences of not considering appropriate genetic sources for revegetation projects (Chapter 7).

The organization of DNA

The basic unit of genetic diversity is DNA, deoxyribonucleic acid, which contains the genetic code. The code provides the programs that determine the function and the form of every living organism and how it interacts with, and is influenced by, its environment. The first level of genetic variation is represented by small differences in the DNA code, which resides in cells of the plant body. There can be differences in DNA within individuals among compartments of a single cell and on different chromosomes, among individuals, among populations, and among related sets of populations.

Each cell contains a number of compartments, some of which are enclosed in a membrane (organelles), and some of these organelles contain the DNA. Most DNA resides in the nucleus (usually the largest organelle of a cell) within structures called chromosomes, but some DNA occurs in other organelles, including chloroplasts (responsible for photosynthesis) and mitochondria (responsible for powering the cell). The DNA in these different compartments are nuclear, chloroplast (cpDNA), and mitochondrial DNA (mtDNA), respectively. This is one way plants differ from animals, fungi, and many microorganisms: plants have an additional package of DNA—in the chloroplasts. Each kind of DNA is passed on by a different mechanism into the next generation.

Genes. DNA is organized into units of information that we call genes. A gene “locus” is the segment of DNA on a particular chromosome that represents a gene. Often, the words “gene” and “locus” (and their pleural forms “genes” and “loci”) are used interchangeably. Individuals have many genes that control the function and expression of their traits. Some traits are controlled by a single gene locus while others are controlled by few to many loci. A trait can be a particular character such as height or color, or it can be a particular functional attribute, such as flowering time, growth response to light, or seed dormancy. In the case of mitochondrial DNA, most of the genes regulate energy and metabolic processes.

In animals and most plants, there are two sets of chromosomes—one set contributed by the maternal parent and the other half by the paternal parent. Species vary in the number of chromosomes they carry, and in plants, even in the number of sets. If there are two sets (the typical condition), this is referred to as a “diploid” individual. If there are more than two sets, the individual is said to be “polyploid”. A polyploid individual with three sets of chromosomes is called triploid, with four sets is tetraploid, and so on.

Allelic variation. The two copies of a gene that reside on partner chromosomes are called alleles. So every diploid individual has two alleles for each gene. These two alleles can be the same, but they are often different. Imagine a gene that controls a particular trait, for example type of leaf pubescence (long versus short hairs). In one population, the gene has two different alleles, represented by the letters “A” and “B”. In the population, there can be three different kinds of diploid genotypes represented: “AA”, “AB”, and “BB”. If both chromosomes carry the same allele, as in “AA” and “BB” genotypes, the individual is said to be homozygous for the trait. If the individual carries a different allele on each partner chromosome, as in genotype “AB”, then it is said to be heterozygous for the trait.

In the leaf pubescence example above, some populations may have additional alleles represented at the leaf pubescence gene. Then, an individual might carry a “C” allele that codes for a different type of hair structure, perhaps one with glands at the tips that exude defensive compounds that deter herbivores (a glandular hair). In this case, there would be three additional genotypes possible, including “AC”, “BC”, and “CC”. If each allele is expressed, then each genotype will have a different type of leaf pubescence (a different phenotype). Now consider hundreds of other loci that control leaf, flower, stem, and physiological traits. If many genes have more than one allele, there will be many possible genotypes in the population. This allelic variation is the basis of genetic variation and is the root level of genetic diversity.

Types of traits

Discrete traits. Some genes control single traits, in a one-to-one correspondence. Such traits are called “discrete“ or “qualitative.” For example, variation in flower color of the slender clarkia (*Clarkia gracilis* (Piper) A. Nels. & J.F. Macbr.) is controlled by allelic variation at a single gene (Gottlieb and Ford 1988). In another leaf pubescence example, where a single gene controls the form of the hairs, one allele codes for short hairs without glands (simple hairs) and another allele codes for glandular hairs. The individual that is homozygous for either simple or glandular alleles would have either velvety or sticky leaves, respectively. If no other gene modifies this effect and the two alleles have equal influence on the trait (if they are “codominant” and additive in their effects), then a different type of hair will occur, or both hairs will be expressed. The result is a third phenotype. However, if there is interaction among alleles and one is “dominant” to the other, then the pubescence would be sticky if the glandular hair allele is dominant or weakly sticky if there is incomplete dominance. In a native jimson weed from the southwest (*Datura wrightii* Regel), leaves have either a velvety pubescence or a sticky, glandular pubescence. The glandular allele is dominant to the velvet allele so heterozygotes have the sticky phenotype. In this plant, the sticky hairs protect the leaves from herbivory (Hare et al. 2003).

Quantitative traits. Often, the situation is far more complex where two or more genes work together to influence a particular trait or a particular gene affects more than one trait. Traits controlled by multiple genes are “quantitative traits” and these are much more difficult to measure. In the case of flower color, more than one gene is often involved. One gene and its set of alleles might code for the pigment (red or blue) and another gene might code for a chemical that modifies the brightness or expression of the pigment. In addition, some genes influence more than one trait. For example, some genes that code for flower color also code for stem color (for example in some columbines and morning glories). And finally, the two (or more, in the case of polyploid species) copies of a gene (alleles) in each individual plant may interact in various ways—from simple addition of the two individual effects to more complicated interactions and less predictable outcomes or traits. Generally, the more genes involved, the more continuous the variation in phenotypes. The environment can also modify expression of many genes, complicating the genetic basis of quantitative traits.

Differences among individual plants can take many forms and often have at least some genetic basis. Some plants are taller or are of different stature than others. The leaves tend to vary in size, shape, margin traits, and sometimes color. Individuals may differ in their stage of seasonal growth, that is, in their “phenology.” For example, you may find a few plants with many flower buds but few open flowers, more plants with few buds and many open flowers, while still others with no buds but plenty of open flowers and some immature fruits. Some of the plants even have flowers that differ in form or color from those on other nearby plants.

Other differences are less obvious such as differences in fragrance, mating system, defensive chemistry, if palatable to herbivores, growth rate, physiology, and chromosome number. Despite the many possible kinds of differences, most individuals from the same or nearby population will be similar enough to each other to be easily recognized as the same species. However, some individuals can be so different from the rest, for example they might have a different stature or flower color, that you might attempt to classify them into a different species. It is much more likely to find the big differences among individuals from populations that are isolated from each other (that is, seeds and pollen are not exchanged, and therefore there is no “gene flow” among the populations) than among individuals from the same population. This is because individuals from the same population tend to share more genes and environments in common.

Gene transmission and reproduction

Nuclear DNA is distributed equally into gametes during the process of “meiosis.” The formation of gametes from the diploid organism is a very precise process that results in only one partner of a pair of chromosomes ending up in the egg cells within the ovule and sperm nucleus within pollen tubes. This process results in reduction from the “diploid” state of an angiosperm or gymnosperm to the “haploid” male and female gametes.

Pollen carries the male sperm cell nucleus (male gamete), and therefore only half of the total DNA content of a mature seed plant. Pollen is dispersed in various ways (by wind, water, or animals) to the ovules of female cones (in conifers) or to the stigmas of flowers (in flowering plants) during the process of pollination. After the pollen is deposited onto the receptive area of the recipient plant (= pollination), the pollen produces a pollen tube that grows through receptive female tissues to deliver the male gamete to the egg cell. At this point, fertilization (the union of gametes) can occur to form the zygote. The zygote then develops into the embryo within the seeds. The seeds develop on the female parent (within the female cones of conifers and within the developing fruits of a flowering plant) and are exposed to the immediate environment of the mother plant. Interestingly, there are various stages between pollination, fertilization, seed maturation, and seed dispersal that can have a large influence on the success or failure of the new sexually produced individuals.

The different kinds of DNA are passed on to the next generation (inherited) a bit differently from each other. The DNA in the nucleus is inherited from both parents. However, for mtDNA and cpDNA, the mode of inheritance varies in different species. In general, in angiosperms, mtDNA is inherited from the maternal parent, whereas cpDNA is inherited either from both parents or the maternal parent. Among gymnosperms, however, there are more variations. In the pine family (Pinaceae), many of the species that have been studied (for example, loblolly pine, *Pinus taeda* L.), show maternal inheritance of mtDNA and paternal inheritance of cpDNA. However, this is not necessarily a valid generalization for all gymnosperms. Coast redwood (*Sequoia sempervirens* D. Don Endl.) has paternal inheritance of both mtDNA and cpDNA (Neale et al. 1989). These different modes of inheritance are important for several reasons. First, they emphasize the high degree of diversity among plant species. Second, they provide a cautionary note in studying the inheritance of traits in plant species: the mode of inheritance should be determined, and not assumed, if results are to be correctly interpreted. Third, these different types of inheritance can be used to gain different kinds of information about a species, including if migration (gene flow) by pollen dispersal differs from migration by seed dispersal.

Genetic redundancy

Within an individual cell, there can be genetic variation and redundancy. For example, genes within the chloroplast DNA frequently code for some of the same enzymes that are coded for by nuclear DNA. There can be some differences in the function of differently coded enzymes, but the compound (substrate) that reacts with a particular enzyme will always be the same one. There is also redundancy in the genetic code. Within each strand of DNA there is a long chain of linked nucleotides (also called bases), of which there are four kinds. The exact sequence of these bases makes up the genetic code. The basic unit of the genetic code is a sequence of three bases and there are 64 possible triplets of the four possible bases. Each triplet of bases codes for an amino acid, and the amino acids combine into proteins, the products of genes. Some triplets code for exactly the same amino acid, as there are only 20 types of amino acids. This means that if there is a mistake in coding or a “point mutation” that substitutes one base for another, some changes will still result in the same functional protein (see mutation below).

Another type of genetic redundancy involves geographically separated genotypes that are adapted to similar environments. Sometimes, very different genotypes from different populations solve a particular environmental challenge in a different way. Genetic redundancy is illustrated by the first generation of distant sources of genotypes (genetically distant ones) sometimes showing high performance when planted in distant locations. Other considerations (more long-term) need to be evaluated before taking advantage of such genetic redundancy.

Measures of genetic diversity within populations

Genetic diversity can be measured in numerous ways—depending on what level of genetic diversity is under study, the type of trait (discrete or quantitative), and analytical methods used. Traits differ in how they are measured and how they are used for quantifying genetic diversity. Table 4.1 provides a list of the various genetic diversity measures described in this chapter. Most measures are standardized and range from 0 to 1. Discrete traits are used to calculate a different set of genetic diversity measures than are quantitative traits. The relevance of the various genetic diversity measures described below to understanding the evolutionary ecology of a single species is increased if they can be compared with measures made on other related plant species. Some values for genetic diversity of several western conifers based on discrete traits are provided in Table 4.2. Even within this selected group of western conifers, considerable variation in genetic diversity can be observed.

Quantitative traits. Continuous variation in height, flowering time, longevity, age to first reproduction, and other quantitative traits is often normally distributed and influenced greatly by environmental factors. Genetic and environmental effects work together to mold a phenotype. To quantify how much of the quantitative trait variation observed is caused by genetic differences among individuals, plants are grown together in a common environment. If the differences are retained when growing together, then there is likely some genetic control of the trait. Sometimes this is done by growing the plants one wants to compare under controlled conditions in a greenhouse or growth chamber.

More naturally, seeds, seedlings, or vegetative propagules are planted outdoors in one or more common field environments. These “common gardens” are usually in a field or test area that has been prepared to be as homogenous as possible. This environmental homogeneity dilutes any variance caused by the environment on the various phenotypes. A common garden experiment performed in more than one environment can be used to estimate the relative amount of genetic versus environmental effects influencing particular discrete traits such as survival and germination (two components of fitness). This is helpful in determining if the fitness of phenotypes differs among environments and from each other (Chapter 6). When a phenotypic trait of a particular genotype differs among environments, the trait is phenotypically "plastic." Trait plasticity is beneficial if it allows individual genotypes to respond in positive ways in different environments. For example, some plants produce large, thin leaf blades when growing in the shade and small, thicker leaf blades in full sun. The higher surface area of the shade leaves allows them to intercept more of the dappled sunlight under a canopy without the danger of overheating. Sun leaves intercept plenty of light in situations where large, thin leaves might overheat. A common growing environment dilutes such differences among phenotypes due to plastic traits and allows one to "see" genetic differences. With appropriate replication and choice of planting design (for example planting replicate genotypes of several clones or multiple siblings from each of several mothers in a random arrangement), the traits of interest are then measured over time. Statistical analysis of the data is done in such a way (for example, "analysis of variance" referred to as ANOVA) to separate genetic and environmental effects on variation.

The genetic components of variation (that is, the variance components) revealed in a common garden study are important to understanding the potential long-term sustainability of populations and their potential to track environmental changes. Traits can be evaluated together with environmental variables to reveal potentially adaptive differences among populations. Furthermore, as will be seen in the next section and in Chapter 6, measurements of quantitative traits can be used in different kinds of genetic diversity analyses. Complex statistical models can evaluate more than one plant trait, environmental variable, or both, simultaneously. Such multivariate models are described in numerous papers that evaluate seed transfer zones for trees (references in Chapter 6).

Common garden experiments often reveal the proportion of phenotypic variance ($h = G/P$), that is genetically determined; this is a measure of the "broad-sense heritability" of the trait, where h ranges from 0 to 1. A value of 1 implies the variation in the trait is completely controlled by genes, and a value of 0 implies the variation is completely controlled by environmental factors. In experiments that include progeny of known genetic relatedness (the pedigree), the G portion of genetic variance can be further broken down into additive (A) and non-additive (dominance, D and interaction, I) components of variance ($G = A + D + I$). The proportion of A out of the total phenotypic variance represents h^2, the "narrow-sense heritability." With respect to a particular trait, this value indicates the potential for a population to respond to selective pressures and evolve. The long-term sustainability of populations depends on there being sufficient h^2 for traits that influence fitness in significant ways, such as timing of leaf flush, for selection to weed out unfit genotypes and increase more fit genotypes over time.

For both discrete and quantitative traits, individual or collections of phenotypic traits can be examined for genetic diversity as represented by the G component of the $P = G + E + G \times E$ equation mentioned earlier. As mentioned in the preceding paragraph, the G proportion of phenotypic variance can be partitioned as $G = A + D + I$. This is also a simplification. There are additional effects that can be added to the equation, such as genetic effects inherited only through the mother or father (maternal genetic or paternal genetic effects). Also, the I term for epistasis can be further broken down, where I = A x D + D x A + A x A + D x D. In this equation A x D, for example, represents the interaction between additive and dominance components of variance. In the field of quantitative genetics, the experiments and statistical analyses become very complex if evaluating the I component, especially if also evaluating effects of multiple environments and possible interaction between genotypes and their environments (G x E). For many years, the epistasis (I) component was assumed to be small and of little consequence. However, recent theoretical developments and computer programs have allowed researchers to further evaluate the role of epistasis. They have been finding that it is more important than previously believed (Wolf et al. 2000).

As will be explained in Chapter 6, the common garden concept is also important in identifying the presence of adaptive differences. This is usually done by comparing the phenotype in more than one environment and seeing if the differences correlate with changes in survival and reproduction. Adaptive differences are revealed if 1) different populations (or genotypes) respond in opposite ways to different environments, and 2) the populations each achieve higher fitness at their home locations. It is best to compare more than two populations and environments at a time to avoid having a 50/50 chance of an outcome consistent with local adaptation. Common garden studies can also be used to examine if particular traits are correlated genetically. For example, tolerance to herbivores may be correlated at the gene level with a lower tolerance to a particular fungal disease, a lower growth rate, or cold tolerance. If traits are genetically correlated, a shift in one trait caused by some environmental factor will indirectly influence changes in any genetically correlated trait.

Discrete traits. Another common method of measuring genetic diversity is analysis of molecular markers that represent discrete genetic differences. Some discrete morphological markers (especially when codominant) can be used in a similar way. The most common molecular marker measured is allozyme variation (see Chapter 5 for more about allozymes and other molecular markers). The method of allozyme analysis, available since the late 1960s, distinguishes genetic variation that is expressed in different "allelic" forms of certain proteins. Thus, while not measuring the DNA directly, this method measures protein differences at a particular gene locus that are caused by small differences in DNA (such as a single base change mentioned above)—so this is just one step away from direct measurement of DNA. There are many different loci with allozyme variation (the different loci are often called "isozymes"). Allozyme variation can be detected quickly by doing a biochemical analysis of a random sample of about 20-50 individuals from one or more populations. Multiple loci can be examined at one time. The analysis provides data on the number and frequency of different codominant allozymes (alleles) at each locus examined. This complete accounting of allelic variation allows the estimation of numerous parameters that provide information about genetic diversity, relatedness of individuals, the mating system, gene flow, genetic similarity of populations, and how alleles and genotypes are distributed geographically. This also allows quantification of the effect of single alleles and revealing if alleles are neutral in their effects.

Allele frequencies (p's and q's) and percent polymorphic loci (P). Based on allozyme differences, the amount of discrete genetic variation within a population can be characterized in several ways. First, it is important to see if in the total sample of individuals the allozyme locus (the gene) is "polymorphic" (has more than one allele in the population) or if it is "monomorphic" (has only a single allele). One common measure is to simply determine the fraction of various allozyme loci that have more than one allele (the percentage of polymorphic loci, P). In practice, a locus is considered polymorphic if its most common allele is represented by a frequency of less than 0.95 (or sometimes by 0.99 as in Table 4.2). To determine this, the number of each allele needs to be counted for each sample locus. Then, by locus, every allele can be assigned a value that represents its proportion out of all the alleles in the sample. For example, if there are 100 individuals, there are 200 total alleles at any particular locus in a sample of diploid plants. If at a particular locus, a certain allele, called "p" makes up 50 of the 200 total alleles, the relative frequency of p is calculated as p = 50/200, or p = 0.25. Other alleles at the same locus are also represented by a relative frequency and are assigned a different letter. If there are only two alleles, the second allele occurs 150 times out of 200. This second allele, "q" can be calculated as q = 150/200, or as q = 1-p = 0.75.

Heterozygosity (H_e and H_o). One can also determine, for each individual plant sampled, the proportion of heterozygous loci of those examined. A diploid plant is said to be heterozygous at a locus when it carries two different forms of the protein at that locus. This value is then averaged over all individuals sampled in the population and expressed as the average "observed heterozygosity" (H_o) for that population. A value of average "expected heterozygosity" (H_e) can be determined from the allele frequency data. Expected heterozygosity is calculated from the relative number of each type of allele and the probability that the alleles are organized into heterozygous versus homozygous individuals. The probability is based on a model that assumes random mating and the absence of active evolutionary processes (selection, migration, random genetic drift—see below). A significant difference between observed and expected heterozygosity yields information important to understanding any detected pattern to the genetic variation in populations. H_e is probably the most commonly used expression of genetic diversity within plant populations.

Allelic diversity (A). A third type of diversity measurement is the average number of alleles per locus (A). This measurement tends to represent more of the allelic diversity, but clouds the issue of how that diversity is distributed. From this measurement alone, it would not be possible to distinguish between a mainly monomorphic population with a few loci with many alleles, and one in which most loci were polymorphic but with only two or three alleles per locus. For this reason, allelic diversity is often represented as a frequency distribution—with the population represented by a table or histogram showing the relative frequency in three or four allele classes, ranging from highly polymorphic to monomorphic.

Inbreeding coefficient (F). Another basic measure of genetic diversity within a population is the level of inbreeding. This value measures the degree of homozygosity, that is, the degree of mating among relatives. This does not reflect the allelic diversity per se, but rather how the alleles are distributed within individuals. It is a measure of the expected level of heterozygosity (H_e) in the population under the assumption of random mating, relative to the observed level of heterozygosity (H_o). It is represented by the "inbreeding coefficient" (F), which ranges from 0 (all individuals heterozygous and therefore no inbreeding, or high heterozygosity) to 1 (no heterozygotes, high level of inbreeding, or high homozygosity). Note that in a completely outbreeding and randomly mating population, relatives can still mate, so we still expect a certain level of homozygosity, which is the opposite of heterozygosity. The inbreeding coefficient is calculated as $F = (H_e-H_o)/H_e$.

Measures of genetic diversity among populations (measures of genetic structure)

When more than one population is measured for patterns of genetic variation, it is possible to quantify how the within population variation is distributed relative to the total variation of all the sampled populations. Measures of genetic diversity that include an “among population” component are often referred to as “population structure” because they reveal if there is a non-random pattern to the distribution of genotypes over the sampled geographic space. For example, imagine a species that has individuals with three different flower colors. White flowered plants are homozygous for the W allele (genotype WW), red plants are homozygous for the R allele (RR), and pink flowers are heterozygous (RW). If we took 4000 red plants, 4000 white plants, and 2000 pink plants, mixed them up and distributed them at random into 12 populations, the variation within populations would be as much as the variation between populations. This would be a set of populations with no significant genetic structure with respect to flower color. If, in contrast, four northern populations were composed of red individuals (monomorphic for flower color), four southern populations were all white (also monomorphic), and the central populations were 40% red, 40% white, and 20% pink (polymorphic), we would immediately see a pattern. In this second case, there is more variation among populations than within populations, and there is significant structure. Structure can be measured with either discrete traits (usually molecular and expressed as a proportion of total genetic variation or as a descriptive statistic) or quantitative traits (usually expressed as variability or a variance). These measurements can have very different meanings because the variation represented by these different types of traits differ in effect on fitness (see adaptive versus neutral genetic variation in Chapter 5).

Quantitative traits and Q_{ST}. Quantitative traits are most often measured to determine heritabilities of traits and if there are significant differences among populations for genetically controlled phenotypes. However, they can also be examined to reveal pattern and structure similar to the use of allozyme and other molecular marker variation (see below). If individuals from more than one population are planted in the same common garden to measure quantitative traits, there will be a hierarchy of relatedness represented among the experimental individuals. Members of a clone are more related than full siblings, full siblings are more closely related than half siblings, and half siblings are more closely related than siblings from different families. One can measure variation among individuals of the same family (or clone), variation among families (or clones) within populations, and variation among populations. The total variation in a trait can then be partitioned into how much is explained by differences among individuals within families, among families within populations, and variation among populations. Results from common-garden studies can then be expressed in terms of the percentage of quantitative genetic variation that is attributable to a certain level in the genetic hierarchy for that species. For example, a result could be that 25% of the total variation in a trait was “among populations”—a measure of the genetic structure of a species. For quantitative traits, this proportion is called Q_{ST}.

Allozyme variation, F_{ST}, G_{ST}, and genetic distance. As shown for quantitative traits and the measure Q_{ST} above, the organization of molecular genetic variation can also be studied to determine if there is a hierarchical spatial pattern. The statistics F_{ST} and G_{ST} are similar and commonly used measures of the proportion of total allozyme variation (or other DNA marker variation, see below) due to differences among populations. The measures G_{ST} and F_{ST} are based on the hierarchical arrangement of allelic diversity. Both measure the variation among populations relative to the total variation. G_{ST} uses values of expected heterozygosity, where H_T is the expected heterozygosity over the total sample (all the populations in a sample), and H_S is the average for the individual populations (and represents the within population diversity). The proportion of variation due to differences among populations relative to the total heterozygosity can be calculated as $G_{ST} = (H_T - H_S)/H_T$. The other measure, F_{ST}, is calculated differently than G_{ST}, and has some subtle conceptual differences, but for our purposes, G_{ST} and F_{ST} provide essentially identical values. Any combination of hierarchical organization can be addressed (for example, subpopulations, populations, regional populations, different subspecies), and so these analyses are very much dependent on the spatial scale of sampling. Because fewer genes are normally exchanged among widely separated populations then close by populations, the larger the scale of sampling, and distance between populations, the more likely it is to see a larger value of F_{ST} and G_{ST}.

In all of these hierarchical measures (Q_{ST}, F_{ST}, and G_{ST}), the subscript "ST" refers to the levels compared in a hierarchy, and all are relevant to the section below, "Structure of Genetic Diversity". For all these statistics, a value of 0 means the variation is distributed randomly in space, that is, all of the variation observed for the total sample is due to differences among individuals within a population and none is due to differences among populations. For F_{ST} and G_{ST}, this means that all populations have the same alleles and allele frequencies. In contrast, the maximum value, 1, means that all the variation is due to differences among populations.

When comparing two or more populations, indices of genetic identity (genetic similarity and its inverse, genetic distance) are the most widely used for comparing allele frequencies. The value for genetic similarity for a pair of populations varies from 0 (no alleles in common) to 1 (identical alleles at every locus and equal allele frequencies at every locus). The index of genetic distance is the reverse of this, so 1 represents the maximum variation among populations.

Other molecular traits. Additional information on genetic diversity comes from studies of mtDNA and cpDNA (these forms of DNA are usually inherited though only one parent). Because of the different inheritance modes and evolutionary histories of the DNA in these organelles, they provide different insights into the genetic diversity of the species. Because the results from genetic studies of these types of DNA may give different kinds of information than that of nuclear DNA, the results are sometimes interpreted as "inconsistent" or "conflicting". However, that is not the case. Rather, they give different kinds of information—which together add up to a more complete picture of the nature of that species' genetic diversity. For example, we might expect studies based on mtDNA to show stronger genetic differentiation among populations (as compared with nuclear DNA). This is because mtDNA may have lower rates of sequence mutation, small population size, and there may be more limited gene flow for maternally inherited organelles (Birky 1988).

Processes affecting genetic diversity

Although all (new) genetic variation ultimately arises from mutation, it is the distribution of these mutations which determines the pattern of genetic variation within the species. There are five general processes that affect the amount and distribution of genetic variation within a species. All of these can influence the formation of genetic structure in populations:

1) Mutation. A mutation is any change in the genetic code. Most mutations are deleterious and in somatic cells and are never passed on. If the mutation ends up in the germ cells—the cells that undergo meiosis to produce gametes for sexual reproduction—the mutation will be inherited. Mutations in somatic cells—the cells of the plant or animal body that never undergo meiosis are not passed to the next generation of individuals, but they can sometimes proliferate within individuals. If a mutation occurs in a meristematic cell, such as in a root tip in an aspen clone, it could eventually lead to inherited traits in the subsequent stems (and their seed).

Plastic changes in phenotypes mentioned above that occur in response to the environment are not mutations and are not heritable, but the ability of a trait to be plastic may be heritable. One kind of mutation is simply a small point change (a point mutation) in the DNA due to a replacement, duplication or deletion of one pair of nucleotides (bases). Another class of mutations results from changes in chromosome structure. Examples include movement of a section of DNA from one location in a chromosome to another (as in "transposition mutations" or "translocations") and the breaking and rejoining of a fragment of DNA in a reverse configuration, a so-called "inversion" mutation. Other chromosomal mutations include changes in the number of chromosomes (ploidy). Such changes can involve addition or deletion of DNA, and fission or splitting of chromosomes. Any of these changes in position and quantity of DNA can have effects on the expression of genes (changes in products) and resulting phenotypes.

Although certain environmental conditions can increase mutation rates, spontaneous mutations continually occur at low rates in nature, continuously adding to the genetic variability in natural populations. Many mutations are lethal, sub-lethal (deleterious) and are eventually removed from the population gene pool because the mutant individuals die before they can reproduce or else suffer lowered reproduction. Some mutations do not affect the immediate viability of the plant (that is, they are neutral in effect) and they may increase in frequency in the population by chance. Occasionally, new mutations are superior to existing alleles. These variants become part of the genetic variation of a species. One example, but not necessarily a "new" mutation, is the gene for resistance to white pine blister rust in sugar pine (*Pinus lambertiana* Dougl.). Another advantageous mutation is that for resistance to the fir engraver (insect) in white fir (*Abies concolor* (Gord. & Glend.) Lindley).

Occasionally, an adaptively valuable mutation might mark the beginning of a new subspecies or species, especially if the change results in reproductive isolation of individuals that possess different alleles. For example, the most prominent differences among columbine species (*Aquilegia* spp.) are floral characteristics, such as nodding or erect position, and presence or absence of floral spurs. Both of these traits are due to single genes (Prazmo 1965). These characters led to the sub-division of the ancestral species as they adapted the species to pollination by different groups of insects and birds (Hodges and Arnold 1994).

2) Natural selection. This is considered the most influential evolutionary process as all adaptive change is the result of natural selection. It operates through differential survival and reproduction of individuals that have different genetically determined traits—better adapted individuals survive and reproduce in their current environment. There are many examples of selection causing adaptive genetic change in native plant species of Region 2, such as adaptation to differences in elevation, climate and soil. Populations of sky pilot (*Polemonium viscosum* Nutt.), for example, show differentiation in flower size and fragrance among elevations that is in part genetically determined. In a series of studies, the different forms were shown to vary in response to herbivory, drought, and use by different types of pollinators (Galen 1989, 1990, 1999, 2000). In addition, F_{ST} values of 0.015 and 0.069 were significant for populations separated by 1.5 km and 1,500 m elevation suggesting limited gene dispersal between sweet and skunky-scented populations. Reciprocal transplants between the sites showed significant home site advantage, a strong indicator of local adaptation (Galen et al. 1991). There are also many examples in forest trees. In ponderosa pine (*Pinus ponderosa* Laws var. *scopulorum* Engelm.), there is evidence that length of the frost-free season and patterns of precipitation drive variation in shoot elongation and other traits in populations from the Upper Colorado River Basin (Rehfeldt 1990). Similar adaptive patterns were found for provenance tests of California populations from a steep elevational transect (in var. *ponderosa*). Adaptive characteristics of higher elevation habitats include slower growth and frost-resistance features (Conkle 1973, Namkoong and Conkle 1976).

Some of the earliest and most comprehensive studies of natural variation and natural selection in plants were conducted in California by a group of scientists from the Carnegie Institution, (Harvey Hall, Jens Clausen, David Keck, and Wiliam Hiesey) from 1922-38 (Clausen et al. 1940). Working with numerous native genera, they transplanted clonal replicates from various habitats to nine common gardens along a California transect extending from the Pacific Ocean at San Francisco Bay, across the Coast Ranges, San Joaquin Valley, and Sierra Nevada Range to the Great Basin at Mono Lake. Plant response to the great variation in elevation, rainfall, temperature and light encountered along this transect allowed insight into the nature of plant distribution in relation to the environment, and in particular, the differentiation into differently adapted phenotypes. In this work, they identified discontinuities in phenotype that were genetically based and that appeared to be correlated with environmental differences. These were called “ecotypes,” a word coined by Turesson (1922), a pioneer of modern common garden studies. They discovered various ecotypes that differed in numerous morphological traits and phenology. For example, four distinct ecotypes were recognized in the widespread species complex, *Potentilla glandulosa*, corresponding to different elevational zones.

There are many examples of natural selection in annual species adapted to elevation and soil conditions. A classic example of soil differentiation is the genetic determination of copper tolerance in some grasses and species of *Mimulus* (for example, *Agrostis tenuis* Sibthorp, *Mimulus guttatus* DC.) growing on mine spoil dumps (Bradshaw 1984, Macnair and Cumbes 1989). Metal tolerance is common in mine populations, but almost completely lacking in adjacent populations growing on normal soils; despite gene flow across the abrupt environmental boundary, differentiation is maintained by strong selection.

It is important to keep in mind that natural selection cannot predict the future. The plants that survive to reproductive maturity (barring chance events) are those that are best suited to current conditions, and their progeny will reflect adaptations to those same conditions. Changes in environmental conditions can be reflected in successive generations, but there is always a lag. An analogy from Alice in Wonderland is often used for this lag in adaptation. The Red Queen, who runs as quickly as she can just to stay in the same place, is a reflection of a species always “chasing” the environment just to maintain a constant level of adaptation. One lesson here is that phenotypes we see today may have evolved under conditions no longer present. This is particularly relevant to long-lived plant species where individual lives may span centuries.

Finally, natural selection can occur at every stage of a plant's life, from seed maturation, germination, seedling survival, and through to reproductive maturity. During reproduction, natural selection influences not only which adults will contribute genetic material to the next generation, but also the genetic composition of the next generation of seeds by influencing differential pollen survival and fertilization success. The fractional success of different genotypes at these main life-cycle stages has a cumulative effect on the genotype’s fitness, and the total fitness of each genotype is the expected contribution of progeny to future generations. It is possible to detect natural selection and identify the most vulnerable stages of growth as affected by a particular selective force by measuring the relative success of genotypes at each life-cycle stage. Estimating total fitness (sometimes referred to as cumulative fitness) requires incorporation of effects at each stage of the life cycle. The effects are multiplicative.

3) Migration. Migration refers to the dispersal of genes through space and time. Spatially, plant genes typically "migrate" within pollen or seeds. In the case of clonal plants, genes can also migrate by vegetative processes such as sprouting from a stump, rhizomes, root sprouting or even the rooting of fallen twigs (for example, in some poplar species). Some species produce specialized vegetative propagules that detach and disperse with the help of animals or water. For example, corms may be harvested and cached by rodents, the tiny bulbils of *Polygonum viviperum* L. that are produced in place of some flowers can disperse like seeds, and pieces of rhizomes or branches of riparian species can beak off and wash downstream. Sexually reproducing plant species vary in their means of pollen dispersal and pollination (primarily by wind, insects, or birds), and whether seed dispersal is primarily by gravity, wind, or animal transport. As mentioned in Chapter 3, there is much variation in seeds and seed dispersal capabilities. The method of pollination also affects the pattern and distance of gene migration, which influences genetic variation. For example, hawkmoths and hummingbirds generally have larger flight distances between flowers than small flies and beetles. In wind-pollinated plants, other factors influence the range of pollen transport—from centimeters to kilometers—including pollen size, shape, pollen density, and wind speed and direction. The density, height, and patchiness of available mates and surrounding plants can affect all types of pollen dispersal.

The transmission of genes, from one generation to the next, with respect to the relatedness of mates is called the mating or breeding system. Plant mating systems reflect the amount of outcrossing. The morphology of cones and flowers, the presence or absence of self-incompatibility mechanisms, how the sexes are arranged on plants, and the type of pollinating agent critically affect how much outcrossing occurs. Mating systems should be thought of as a continuum of possibilities rather than as discrete types. Furthermore, mating systems are under genetic and environmental control and are subject to selection if there is genetic variation controlling the mating system. The type of mating system common to the species plays a major role in how genetic variability is organized in populations and the way genetic variation is structured, a topic explored in a later section. Basically, inbreeding leads to lower levels of genetic variation within individuals and populations, and more variation between them (high F_{ST}). Outbreeding produces the opposite effect: variation within populations is high relative to that between populations (low F_{ST}). Plant species exhibit a large variety of such systems.

Most plant species are predominantly outcrossing but there is much variation in mating system (see also Chapter 5). Closely related species or even populations within a species may have different mating systems. For example, the yellow monkey flower (*Mimulus guttatus* de Candole) has a variable mating system in which about half to all of its flowers are outcrossed. In contrast, a very closely related species with smaller, often cleistogamous flowers, *M. nasutus* Greene (sometimes called *M. micranthus*), is predominately self-pollinating (Dudash and Carr 1989, Fishman et al. 2002). In another example (there are many), Grant (1975) reports that *Gilia ochroleuca* M. E. Jones from southern California, occurs from the coastal mountains east into desert habitats. The mating system changes in concert with this range of habitats. Flowers are bee-pollinated and partly outcrossing in woodland communities in the central portion of this range but are self-pollinating in open habitats of the Mojave Desert near the eastern boundary of the species. A selfing race also occurs on the extreme northwestern margin of the species range. One might expect the pattern of genetic variation to change accordingly.

4) Random genetic drift. Genetic drift is a random process. When plants reproduce, the seeds that result do not necessarily contain all of the genetic diversity from the parental generation. The genes from some potential parent plants may not be represented in the seeds because of distance from other plants, weather patterns that influence pollen dispersal, random deaths of plants, random abortion of embryos, and other random factors. In particular, alleles that are rare in a plant population may not be transferred to the next generation, just by chance. As such, the next generation represents a sample of the genetic diversity in the parental population. In a smaller plant population, or in a small sample of propagules, these random processes are even more amplified. For example, rare alleles may be present in only a few individuals, increasing the probability that at some point, by chance, they won't make it to the next generation and will be lost forever from that population. Conversely, in a small population, a rare allele might increase because it happened to occur in the individual that survived a landslide or other chance event. Drift occurs in all populations, but generally, small populations tend to lose genetic variation by genetic drift much more quickly than larger populations, resulting in loci that become "fixed" for a single allele (become homozygous). The shorter the generation time (that is, length of time from germination to reproductive maturity), the more rapid the diversity loss in absolute time (Frankham et al 2004).

When we talk about the relationship between the size of a population and genetic drift, we do not mean a count of the number of "individuals" in the populations. An important concept that involves genetic drift and the structure of populations is effective population size. Effective population size (N_e) is a measure of the number of individuals in a population that contribute genes to succeeding generations. The actual census number of individuals in a population (the census size) is much less important to population persistence and evolution than the number of individuals that actually reproduce. For any particular amount of genetic drift or inbreeding, N_e is the number of individuals within an "ideal" population (that is, a population that is large, random mating, not exposed to selection, equal sex ratio, non-overlapping generations) that would result in the observed amount of drift or inbreeding. For many plants, N_e will be smaller than the number of plants in the population. For example, plants that reproduce primarily by apomictic seed, are highly selfing, or that have very unequal sex ratios will have much lower N_e than the census number. Such traits can be very important when deciding on collection strategies for restoring populations.

Genetic drift in populations with a small N_e may result in populations with unusual variation. Because of these random sampling effects, neutral or even non-adaptive genes can be established in populations.

Two northwestern coniferous species, western white pine (*Pinus monticola* Dougl. ex D. Don) and western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), may owe their current genetic uniformity to genetic drift. Western redcedar, described as having "one of the lowest degrees of variability found thus far in northern North American conifer species"(Von Rudloff and Lapp 1979), may have lost much of its variability during glaciations, when it was reduced to a small population far south of the glacial limits. In the case of western white pine, the northern populations have far less genetic variation than do the more southern populations (Steinhoff et al. 1983). It is speculated that the northern part of its range was reduced during glaciations to a small coastal population, whereas the southern populations in California were less restricted by ice and acted as multiple refugia (Critchfield 1984). The genetic variability lost through this massive reduction in the northern part of the species range has not been regained even with the reoccupation of habitats by migration of the coastal population.

5) Non-random mating. Non-random mating occurs when genotypes or phenotypes pair in a non-random way. Some forms of non-random mating can result in changes in allele frequencies over time and can be included properly as a subset of natural selection. An example is when a particular flower color is favored by pollinators and the allele controlling that color increases in a population. Assortative mating, however, is another type of non-random mating that has effects much like inbreeding and outbreeding. In positive assortative mating, individuals that are more alike mate with each other more than at random, such as when pollinators tend to remain constant to a particular flower color within a foraging bout in a population that has a flower color polymorphism. Positive assortative mating with respect to timing of reproduction commonly occurs because plants that mature flowers or cones early tend to mate with others that mature early and those that mature late tend to mate with others that mature late. This tends to result in an increase in homozygosity rather than a change in allele frequency. In contrast, in negative assortative mating, individuals that are unlike each other tend to mate with each other more than at random. For example, in heterostylous flowers, such as in European blue flax (*Linum perenne* L.) and the primroses (*Primula*), some flowers have long styles and short anthers while others have short styles and long anthers. In such populations, pollen deposition by pollinators is more likely to occur on flowers of the opposite type. The result is an increase in outcrossing efficiency. This can result in a stable polymorphism in flower type and an increase in heterozygosity.

Structure of genetic diversity

Just as biological diversity is appropriately represented as having a hierarchical structure with genetic diversity as its foundation (Chapter 1), genetic diversity, too, can be described as a hierarchy. This hierarchical structure is often referred to as the “genetic structure” of a species, which we introduced under the section about genetic diversity among populations. As this structure is usually described in a spatial context, it is also sometimes called “spatial genetic structure”. Because genetic studies often focus on particular levels of the hierarchy, the term “genetic structure” is often used for the broader scale studies that describe range-wide or regional spatial genetic structure, while the term “fine-scale genetic structure” is applied to genetic arrangements at more local levels—such as among several local populations, or the structure within populations (such as when individuals from a family are clustered in space). Species differ not only in the total amount of genetic variation they contain, but in the way in which this variation is partitioned among these levels. Described below are the various levels in the genetic hierarchy. Some of these have been described earlier, but are repeated here to show the full range of levels.

Individual gene locus. One could describe the genetic variability from the perspective of a specific gene locus. Based on a sample of individuals from a population, one could find that there is no variation at this locus (that is, locus is monomorphic) or that there are two or more variants (polymorphic).

Genome level. This refers to the ploidy level, or number of copies of each genetic locus per genome, discussed earlier. Thus, the ploidy level sets the upper limit for variation at a locus in an individual. For example, if a species is diploid, an individual can have, at most, two types of alleles at any locus. Tetraploids that are formed after the hybridization of two different populations (often different species) and subsequent doubling of chromosomes (called allotetraploids) can have up to four alleles at a locus. Other tetraploids (autotetraploids) are much like diploids and normally have up to two alleles at a locus (read about polyploidy in Box 14).

Individual level. As each plant carries at least two copies of each gene (one on each chromosome) there are many ways for genetic variation to be represented. Each gene could have several variant forms (alleles) and the plant could possess one form (homozygous) or two forms (heterozygous) of each gene. Thus, one measure of genetic diversity is the degree of homozygosity or heterozygosity of an individual based on a sample of its loci.

Within-population level. If a number of individuals from a population are sampled, and their heterozygosity values are averaged, this average heterozygosity (H) can be used as a measure of within-population variation. Another measure is the number of polymorphic loci (the number of genes that have more than one form, usually expressed as the percentage of all sample loci (P) and the average number of alleles or mutants that occur at each locus (A). The number of alleles per locus is often quite low—normally between one and three. The low observed number of alleles per locus is probably often a sampling phenomenon—rare alleles would not often happen to be chosen for analysis. In studies of quantitative traits in common gardens, the variance in a quantitative trait can be partitioned among individuals and families.

Another perspective for genetic variation is the “genotype” frequency—the genotype being the “package” in which the genes reside in an individual, or the genetic constitution of the individual. There are processes mentioned earlier that, while not affecting the total amount of genetic variation in a species (the percentage of polymorphic loci or number of alleles per locus), do affect the distribution of genotypes in a significant manner. For example, positive assortative mating and inbreeding (mating of related individuals) alone do not affect the frequency of alleles in a population. However, relative to outbreeding and negative assortative mating, they change the relative frequency of genotypes in the population. The frequency of homozygotes (the individual possesses only one form or allele of the gene) is increased, while the frequency of heterozygotes (the individual has typically two forms or alleles of the gene) is decreased.

The spatial arrangement of genetic variation within the population is largely a function of the mating system, as described earlier. Outcrossing, wind-pollinated species will tend to exhibit little within-population structure, while more inbreeding types will exhibit a “family style” of structure. The pattern presented by the mating system will, of course, be influenced by natural selection and dispersal of seed and other propagules (see chapter 5).

Seed/propagule dispersal that differs from pollen dispersal can temper structure or influence structure at different spatial scales, including within populations. Wind pollinated trees such as oaks and pines can have distant pollen dispersal coupled with limited seed dispersal. Oaks have very little genetic structure as measured among regional or nearby populations (low F_{ST}), but at small spatial scales can build up family structure, likely due to limited dispersal of acorns (Montalvo et al. 1997). Conversely, a highly selfing species or species with pollinators that move short distances can have wind-dispersed seeds with large dispersal ranges, pushing an otherwise very high value of F_{ST} downward.

Among-population level. Many of the measures used for within-population variation can also be used to compare the relative amount of genetic variation among a species' populations. For example, genetic studies of Torrey pine show this species to have little or no variation within its populations but significant differences between populations (Ledig and Conkle 1983).

In species with high levels of genetic variation both within and among populations, there is a further classification—that of discontinuous or continuous geographic variation. In the former, the genetic differences among populations are abrupt. If these differences appear to be adaptations to abrupt environmental differences, the populations are labeled “ecotypes”. Major ecotypes have been described, for example, for ponderosa pine. Alternatively, where the genetic variation occurs gradually, the pattern is described as “clinal”. There are many examples of clinal variation in native western plant species, where gradients in some environmental factor(s) are reflected in a genetic gradient. For example, ponderosa pine in the Colorado Plateau (including the adjacent areas of the Uinta Range in Central Utah, the San Juan Mountains in southwest Colorado, and the Tushar Mountains) shows clinal genetic variation associated with the length of the frost-free season and patterns of precipitation (Rehfeldt 1990). Early height growth in white fir (*Abies concolor* (Gordon & Glend.) Lind.) and incense-cedar appears to increase clinally from south to north in California. The pattern of variation may be quite different among traits within the same species.

Another non-random pattern that can arise is one that occurs simply due to a combination of inbreeding, mating distances, seed/propagule dispersal, and random genetic drift, or by “isolation by distance”. The pattern can look much like a cline in that there may be an increasing frequency of an allele or genotype the further away one samples from a reference position. A common way to identify isolation by distance, is to look for a correlation between geographic distance and genetic distance of populations. Genetic distance for this test needs to be measured with genetic variation that is not adaptive (is not correlated with an environmental gradient), such as much allozyme variation or other “neutral” variation in DNA (see chapter 5). Often, clinal variation in adaptive traits and isolation by distance in non-adaptive traits are used to infer the evolutionary processes that could have driven the observed patterns.

Evolutionary processes work within hierarchy

The five processes that influence the distribution and pattern of genetic variation (mutation, selection, migration, genetic drift, and non-random mating) act within the constructs of this hierarchical arrangement. For example, natural selection occurs primarily at the individual level through the differential success of different individual genotypes. Mutation and random genetic drift can be regarded as forces that change gene frequencies within populations. Migration, as an interpopulation force, usually causes the genetic constitution of several populations to converge, depending on the strength of the migration. Selection and random genetic drift may oppose the homogenizing influence of migration by causing populations to differentiate from one another. The complex interplay of these four evolutionary forces determines the genetic constitution of a species and, ultimately, whether new species will emerge from the genetic division of a preexisting species owing to the emergence of reproductive isolation barriers.

In conclusion, although the ultimate origin of genetic variation is rather straightforward, its nature within plant species is rather complex. This has two important implications. First, although there are certainly some generalities among plant groups, each species has a rather unique genetic signature—the amount and structure of its genetic variation. Second, in any discussion of genetic variation, the context is all important. An appropriate context should consider a temporal reference point, the genetic structure of the species, and the specific genes or traits whose variability is under discussion. The latter point, in particular, is important as the variability in one gene or trait of a species may bear little resemblance to the genetic variability in others.

Table 4.1. Summary of common statistical measures of genetic diversity within and among populations. G and Q_{ST} are based on quantitative traits. The remaining measures are based on discrete trait variation, usually molecular markers.

Measure	Description	Basis of value
Genetic diversity within populations:		
G	Genetic component of phenotypic variation in quantitative traits	The portion of phenotypic variance controlled by genes
h	Broad sense heritability	% of total phenotypic variance that is due to all forms of genetic variance
h^2	Narrow sense heritability	% of total phenotypic variance that is additive (measures ability to respond to selection)
H_o	Average observed heterozygosity	Observed fraction of heterozygotes averaged over all sample loci
H_e	Average expected heterozygosity	Expected fraction of heterozygotes based on allele frequencies, averaged over sample loci
P	Percentage of polymorphic loci	% of all loci with > one allele
A	Average alleles per locus	Number of alleles/locus averaged over all sample loci
F	Inbreeding coefficient (the probability of alleles being identical, that is, or probability of homozygosity)	The difference between H_o and H_e relative to H_e: $[F = (H_e\text{-}H_o)/H_e]$
Genetic diversity among populations:		
Q_{ST}	Proportion of quantitative trait variation among populations	Relative to total phenotypic variation measured over all populations
F_{ST}, G_{ST}	Proportion of total molecular marker variation among populations, averaged over loci	Relative to variation measured over all populations
Genetic distance	Fraction of alleles and frequencies not shared among pair of populations	Pairwise comparison among populations
Genetic similarity	Fraction of alleles and their frequencies shared among a pair of populations	Pairwise comparison among populations

Table 4.2. Some values for allozyme diversity for western conifer species: mean number of alleles per locus (A), percent polymorphic loci (P), and expected heterozygosity (He).

Species	A	P[1]	He	Reference
Thuja plicata	1.0			Copes 1981
Cupressus macrocarpa	1.2	61		Conkle 1987
Larix occidentalis	1.8	58		Jaquish and El-Kassaby
Chamaecyparis lawsoniana	1.9	65		Millar and Marshall 1991
Taxus brevifolia	2.0	68		Wheeler et al. 1995
Pinus ponderosa [2]		68	0.155	Niebling and Conkle 1990
Pinus albicaulis	2.6	85		Jorgensen and Hamrick 1997
Pinus contorta	2.7	89	0.185	Conkle 1981
Pinus contorta[3]		66	0.17	Yang and Yeh 1993
Pinus lambertiana	2.8	80	0.275	Conkle 1981
Sequoia sempervirens	3.1	92		Rogers 2000
Pseudotsuga menziesii[4]	3.9	74		Conkle 1981

[1] The criterion for polymorphism used in these studies is 99%, meaning that a locus must have a second allele with at least a frequency of 1% for that locus to be considered polymorphic.
[2] *Pinus ponderosa* var. *ponderosa*
[3] *Pinus contorta* ssp. *latifolia*
[4] *Pseudotsuga. menziesii* var. *menziesii*

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Chapter 5

Genetic Diversity and its Relationship with Evolution, Ecology, and Life History Characteristics

Measures of genetic diversity require an appropriate context for meaningful interpretation. If you were presented with a statistic that represented a measure of genetic diversity for a plant species, for this to be meaningful you might want to know:

- Is this statistic a species average?
- Is it typical for all populations of the species or for this type of species?
- Is the diversity randomly distributed or spatially structured in some way?
- Has this number remained fairly constant or has it changed historically or recently?
- What are the plant's breeding and seed dispersal systems that influence how the plants share genetic diversity?
- What method or type of genetic data was used to estimate the statistic?
- Is this diversity related to any adaptive traits?

Presented in this chapter is some of the context that can help make biologically meaningful interpretations of genetic diversity and genetic variation. A brief review is offered of the different kinds of genetic data and methods for assessing genetic diversity. A discussion follows of how a species' evolutionary history and migration patterns can add valuable perspective to genetic information. The various implications of inbreeding within populations and hybridization among populations are assessed by considering those processes within the context of the different breeding systems of species. Results of studies are presented that have compared genetic diversity of various species with their life-history traits such as breeding system, seed dispersal system, successional stage, and mode of reproduction. These comparisons not only make logical connections between genetic diversity patterns and the vehicles that move genes in time and space, but allow us to see where generalizations may be appropriate. This also includes a consideration of the different types of genetic variation, comparing neutral with adaptive variation—the latter often being of greater interest to land managers.

Types of genetic diversity and their meaning

There is a broad suite of methods for measuring genetic diversity. These include quantitative trait data (Chapter 4) derived from well-designed common-garden studies and molecular marker data derived from the random sampling of individuals from wild populations. Molecular data include allozymes which represent variation in an enzyme coded for by a single gene locus, or DNA data that measure variation in the genetic code itself. There is an increasing arsenal of DNA markers available and each yields different information. Commonly used DNA markers include restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPDs), microsatellites, and haplotype-based markers such as DNA sequences and restriction site maps. All these types of genetic polymorphisms can be used to quantify genetic differences among individuals and populations. These different methods reveal different kinds of genetic information such as selective versus neutral genetic variation, random versus selected portion of genome, length of DNA sequence sampled, polygenic (quantitative) versus single-gene variation, and additive versus nonadditive variation. Some contrasts and comparisons among molecular markers are provided in Table 5.1. This is not intended to be a thorough description of all molecular markers nor an instruction guide for their use, but a general outline of the various types and uses of such markers so that they might be more familiar to the Reader when they are encountered in genetics literature.

No one kind of data or method is ideally suited for every biologically meaningful question about genetic diversity (Table 5.1). Each type of molecular marker has its own set of possible biases depending on the statistic being estimated and the underlying assumptions of the statistical model. The most appropriate data will depend on the specific kind of information sought.

The markers and methods also vary in level of difficulty to use (sophistication of equipment and skills required) and expense. But these factors can vary considerably in different contexts and over time with the development of new technologies that can more quickly, accurately, and automatically process samples. Each marker has some associated weaknesses or disadvantages. For example, the interpretation of allozymes is complicated by null alleles. Polyploids can be particularly difficult to interpret. And while many of the enzymes are neutral, some are influenced by selection, complicating the interpretation. In chloroplast (cpDNA) and mitochondrial DNA (mtDNA), there is sometimes too little variation to be useful in detecting differences among samples. The lower amount of variation in mtDNA and cpDNA (relative to nuclear DNA) has been thought to be the consequence of inheritance without recombination although knowledge of the transmission genetics of these genomes is far from complete. RFLPs can be time-consuming and depend on the prior development of a genetic library.

Not only may different methods provide different kinds of genetic information, but the implications of this information may depend on characteristics of the species. For example, in animal species, mtDNA can reveal information on genetic structure that allows separation of patterns of dispersal between the sexes (Rand 1996). This is because mtDNA is maternally inherited in animals and most plants. Using mtDNA analysis and behavioral observations, Boyce et al. (1999) examined genetic structure of home-range groups of desert bighorn sheep (*Ovis Canadensis*) in the Peninsular Ranges of southern California, providing information on how the differing behaviors of males and females contributed to the observed pattern of genetic diversity.

However, this application of mtDNA is not universal. Although maternally inherited in most flowering plants and conifers, mtDNA is inherited through the pollen parent in coast redwood (*Sequoia sempervirens*) (Neale et al. 1989). The situation is even more interesting with the additional plastid genome possessed by plants and other photosynthetic organisms, cpDNA. CpDNA is maternally inherited in most flowering plants, paternally inherited in some (for example, many conifer species), and inherited through both parents in a few (Strauss et al. 1989). This means that it is important to know how the genome is inherited when commenting on the genetic diversity of that genome for a particular species. Then one can make the best use of the available tools and explore differential dispersal of genes through maternal and paternal lines.

Although a comparison of all the types of genetic data and their measurement is beyond the scope of this chapter, the choice of method is important. On a species-specific basis, different genetic markers are valuable for detecting different types of genetic variation and drawing inferences on varying genetic processes. Different markers may sample different areas of the genome and thus require different assumptions and interpretations. For example, most often allozymes are found in the single copy region of the genome whereas RAPD markers are found in both repetitive and single copy fractions (Allegrucci et al. 1995). Thus, if comparing genetic information that derives from RAPD and allozyme markers in different years or from different populations, one must consider that they may be expressing different parts of the genome and therefore not directly comparable for monitoring purposes. Different types of data may also reflect different timescales of influence on the genome because they undergo genetic change at different rates. Allozyme data (based on nuclear DNA) are often considered to reflect long-standing genetic differences. This is also true for mitochondrial DNA (mtDNA), making these data especially useful for detecting the appropriate scale for monitoring or management of a species. Mitochondrial DNA studies are less effective in determining recent losses in within-population genetic diversity (Moritz 1994).

Neutral Variation: Some forms of genetic variation do not result in adaptive differences among individuals. Such variation is neutral with respect to fitness and can be used to estimate historical patterns of gene flow, test for (genetic) isolation by distance, or estimate relatedness among individuals. There are a number of molecular genetic markers that usually, although not always, reflect neutral variation, including allozymes and microsatellites. However, even these sometimes reflect adaptive variation either directly or indirectly. Allozyme markers usually function well in estimation of population genetic parameters that are based on the assumption of neutrality, such as population substructure (represented as F_{ST} or G_{ST}, where higher values indicate greater divergence among subpopulations) and genetic distance (any of several measures of the degree of genetic difference between populations). But allozyme variation can have adaptive value if the variation results in functional changes in the enzyme. For example, in studies of ponderosa pine (*Pinus ponderosa* P. & C. Lawson) in the Colorado Rocky Mountains, an allozyme of peroxidase enzyme (PER) in trees on south-facing slopes had a higher frequency than an alternate allele associated with the cooler, moist north-facing slopes (Mitton et al. 1977). Similarly, differences in allele frequencies for another allozyme—glycerate dehydrogenase (Gly)—are associated with moisture availability in piñon pine (*Pinus edulis* Engelm.), suggesting that this may be adaptive variation (Mopper et al. 1991).

These differences (that is, reflecting neutral versus adaptive genetic variation) among loci can be handled by appropriate analytical procedures. Loci that have adaptive variation can be removed from data sets before running statistical analyses that assume neutrality. Each locus can be screened for patterns consistent with selection, similar to the study on ponderosa pine. For example, different sets of allozymes were found to be correlated with geographic variables and growth traits in sugar pine (*Pinus lambertiana* Dougl.). The results were interpreted to suggest that the former sets of allozyme alleles might reflect historical migration of the species and be more neutral than other alleles, while the latter (growth trait correlates) may be descriptive of natural selection for sugar pine (Martinson 1997). Correlations between allele frequencies and environmental variables can also occur in the absence of selection (as in clines), so a selection hypothesis would need to be verified with experiments. Similar methods can be used to assess potential for adaptive variation in DNA markers such as RFLPs.

Highly variable loci—such as microsatellites—are increasingly popular in evolutionary and conservation-related studies because of their high information content. Variation at these markers is rarely selected, however, they too, have weaknesses depending on objectives and species' characteristics. For example, because the models for estimating population structure and genetic distance were based on a much lower level of variation, the estimation of theses parameters can be biased. This can result in measured differences that are statistically significant but have little biological significance, and *vise versa*. For this reason, Hedrick (1999) recommends using microsatellites for measures that are variation independent.

Adaptive Variation: When the objective is to understand genetically based differences in traits that are related to adaptation such as growth rate, phenology, seed production, drought resistance, and so on, common-garden studies are often used. In this context, quantitative traits that influence fitness can be measured. For example, in a study of Scots pine (*Pinus sylvestris* L.) in Finland, important morphological traits show considerable genetic differentiation between northern and southern populations while molecular markers including allozymes, RAPDs, and microsatellites all show little differentiation (Karhu et al. 1996). In addition, morphological traits usually yield more information about local adaptive differences among populations. This is illustrated by studies with lodgepole pine (*Pinus contorta* Dougl. Ex Loud. ssp *latifolia* (Engelm. ex S. Wats.) Critchfield), in North America, where there was little structure revealed in molecular markers. However, in common gardens, growth traits with significantly higher structure reflected adaptation to superior establishment under different regional photoperiods, precipitation, and temperature Yang et al. 1996).

A comprehensive examination of population differentiation in early growth characteristics of lodgepole pine (including height, survival, freezing injury, rate of shoot elongation, and time of cessation of shoot elongation) from the Rocky Mountains area (representing over 163 populations from Idaho, Wyoming, and Utah) revealed significant relationships between genetic variation and environmental variables, suggesting adaptive variation. Specifically, clinal patterns in variation generally reflected elevational gradients and frost-free periods. Because a given frost-free period is associated with a different elevation in different geographic areas, both must be considered in any choices of appropriate genetic source for a planting project. For example, based on this research, a given level of performance in populations from central Idaho will occur in populations from eastern Idaho at an elevation that is 500 meters higher and in populations from Utah at an elevation approximately 1,000 meters higher (Rehfeldt 1988).

Evolutionary relationships/phylogeography

A recurring theme across these chapters is that genetic diversity is dynamic. Both in space and time, it is constantly changing. Any measurements of genetic diversity are snapshots and require a context for meaningful interpretation. One such meaningful context is to look back in time, to see the evolutionary trajectory of a species. In addition to genetic influences, the contemporary genetic structure of plant species has been influenced also by biogeographic and demographic factors in the past. A relatively new discipline, called phylogeography, considers these factors and provides meaningful cross-linkages between the more traditional fields of phylogenetics and population genetics (Avise et al. 1987). This field has been greatly aided by new genetic technologies. For animals, phylogeographic studies typically have used mtDNA—comparing the genetic relationships among populations, subspecies and species, and plotting these against their geographical distributions (Hewitt 2001). In plant species, both chloroplast (cpDNA) and mtDNA are used—these genomes are slower to accumulate mutations than nuclear DNA and thus reflect more ancient relationships. One reason for the constancy of the DNA in the chloroplast and mitochondria is that the former, and perhaps also the latter, apparently do not experience recombination.

Phylogeography can help in interpreting relationships among various populations of a species. For example, two different species could have the same measure of population genetic structure (see Chapters 3, 4 and 6), but it could reflect very different circumstances. One could reflect fairly recent or contemporary differences between populations—this is called a “shallow” population structure. Alternatively, the measure of population differences could reflect very longstanding, ancient differences between those populations—called a “deep” population structure. Generally, molecular markers that evolve slowly are better at estimating deep than shallow structure.

Phylogeographic studies have now been conducted for many plant taxa. Particularly well represented in these studies are forest trees species which are well-suited to these studies because they are long-lived, often have a broad geographic range, usually have a deep evolutionary history, and often have different modes of inheritance for their three genomes (cpDNA, mtDNA, and nuclear DNA). A phylogeographic study of limber pine (*Pinus flexilis* James), for example, provides evidence that ancient limber pine moved into at least seven refugia during the last glacial maximum, thereafter slowly dispersing from these locales, assisted by Clark’s nutcracker, *Nucifraga columbiana* (Mitton et al. 2000). This process could account for the strongly differentiated populations we see today within that species. A similar study of lodgepole pine (*Pinus contorta* ssp. *latifolia*), revealed phylogeographic patterns that were consistent with a rapid, post-Pleistocene expansion of the species, with current population differentiation being a relatively recent event (Marshall et al. 2002).

Understanding the ancient geographic and genetic histories of a species can assist in interpreting their current geographic status and genetic patterns in a meaningful way. If populations have been separated for a long time, their differences may be more biologically meaningful than for a species whose populations have only recently differentiated (even if they both have the same measure of genetic differentiation among populations). For example, mating incompatibilities and potential for coadaptive differences increase with time since divergence (Edmands 2002). And if phylogeographic information is available for sufficient numbers of taxa in a region, patterns may emerge (such as the coincidence of species diversification and establishment of genetic structure with climatic and geomorphological events) that can offer conservation lessons even for species whose population genetic structures are still unknown (Calsbeek et al. 2003). In summary, knowledge of the evolutionary history of a plant species can help inform plant transfer choices, even in the absence of other kinds of genetic information.

Hybridization

New species arise from various mechanisms. In general, barriers to reproduction (a common way of defining species, although problematic in its application to plants) may arise from geographic barriers that are gradually followed by genetic differences, or by other processes that result in substantial genetic changes within the species. Hybridization is one such process that can result in speciation. It is also recognized that more than one speciation mechanism can operate even within closely related taxa. Rieseberg et al (1990a, 1995) have investigated the relationships and postulated origins for several diploid species of sunflower (*Helianthus* spp.). They concluded that *H. paradoxus* Heiser and *H. anomalus* Blake have hybrid origins, having arisen from crosses between *H. annuus* L. and *H. petiolaris* Nutt., while *H. neglectus* Heiser seems to be a recent non-hybrid species derived from *H. petiolaris*.

Although hybridization among species is considerably more common in plants than animals, it is fairly common in the latter and especially common in fishes with external fertilization (Avise 2004). A thorough census of hybridization across all plants species has not been done, but one survey suggests that although hybridization is common in plants, it is not a uniformly common event among all vascular plant species. Ellstrand et al. (1996) inspected five floras (including those of the Great Plains and the Intermountain West) and found that some families and genera had much higher frequencies of hybridizations than others (Table 5.2). These genera may be considered hot spots of contemporary hybridization. In general, the groups that had high frequencies of natural hybridization are characterized as outcrossing perennials with types of reproduction that can stabilize hybridization (such as vegetative reproduction, production of asexual seeds, or polyploidization). At least 21% of the Great Plains families and 31% of the Intermountain West families have species that exhibit natural hybridization. It is interesting to note that all of the hybrids within the *Verbenacea* are within one genus (*Verbena*), whereas only a third of the hybrids within *Asteraceae* are within the Aster genus. Conversely, some families have no reported hybridizations.

Although hybridization often results in mixed genomes, sometimes there is an unequal contribution of nuclear DNA from the parents, and the chloroplast or mitochondrial DNA is usually contributed from only one parent. Also, many hybridizations between species or subspecies result in significantly fewer seeds or more sires by one population of the cross than the other, providing an opportunity for backcross hybrids with nuclear DNA from one parent and plastic DNA from the other parent. This “cytoplasmic genomic capture” can be used to trace recent or ancient hybridization between the two parental species or subspecies. Many such cases of interspecific genome capture have been reported in plants (see Table 5.3). This phenomenon is also important to recognize because it shows that if we study both genomes involved in a putative hybridization event, we may be able to unravel the evolutionary history of a new species, subspecies, or other divergent population. Information about the evolutionary history can help in assessing which populations might be compatible and good choices of plant materials for particular revegetation projects and which might be ill-advised.

Sometimes populations of one species that have diverged over time and become two separate species, reconnect. This is called secondary contact. This contact may be through natural migration or influenced by humans (anthropogenic migration) such as when we use distant populations for restoration. If upon secondary contact mating occurs, the compatibility of the hybridized populations is expected to be lower the longer the populations had been separated. (Note that the term “hybridization” is used to embrace any cross between genetically differentiated forms, within or between species.) However, the success of hybrids will be affected by the particular genetic architecture of the combining populations (Waser 1993, Wade 2002, and others). The mechanisms that cause incompatibilities among hybridizing populations will influence the continued divergence, merging, or extinction of populations over a range of environments.

In summary, hybridization is a natural process. It typically occurs over long periods of time. Natural hybridization can contribute significantly to longer-term evolution in two basic ways: by transferring nuclear DNA which results in genetic combinations, or direct transfer of plastid genomes and possibly new adaptations, from one taxon to another. If the transfers are beneficial, there may be an opportunity for the creation of new lineages. Natural hybridization is a major historical and current speciation process. However, many hybridizations in nature are probably unsuccessful and don't result in viable progeny or ultimately in new species. The key is to avoid translocating plants such that hybrids might be produced that are unstable, infertile, or otherwise ill-adapted to local environmental conditions.

Hybridization events that we initiate, through translocations of plants among populations, for example, have a different context for interpretation than that of purely natural hybridizations. They occur over relatively short periods of time. And the probability of seeing beneficial exchanges is expected to be very low for unnatural hybridizations among distantly related populations (such as those that can occur when plant populations are introduced from different climatic zones in revegetation projects). Obviously, hybridizations are less likely in self-compatible plants and more likely in obligate outcrossers. Hybridizations could have either positive, long-term outcomes, or less desirable ones (see the following section on inbreeding and outbreeding depression). Currently, there is no easy way to predict the result of hybridization among a set of differentiated populations—towards improved fitness, no change, or lower fitness. The outcome is dependent on numerous factors, including the particular underlying genetic architecture of the combined populations, environmental adaptations of the populations, and environment available to the hybrid generations.

Inbreeding and outbreeding: deleterious, advantageous, or insignificant?

What is inbreeding and outbreeding? All individuals of a species are related to each other to different degrees. In a single population, some individuals are very closely related (such as siblings or parental-progeny relationships) and others are very distantly related (such as distant cousins). In clonal organisms, separate stems of the same clone are all the same individual (although there can be genetic differences that result from somatic mutations). The degree of inbreeding that occurs when individuals mate, will then be determined by how much genetic material the two mates share in common. The inbreeding coefficient (f), reflects the probability that the alleles obtained from each parent have a shared ancestry (concept introduced in Chapter 4). This probability is influenced by the relatedness of the mates, the mating behavior of plants, and how much the mating behavior deviates from completely random mating. Inbred matings (and mating or breeding systems) are those involving mating between individuals that are on average more *closely* related to each other than by chance alone. In contrast, outbred matings are those that are among individuals that are more *distantly* related than would occur by chance.

The most extreme form of inbreeding is represented by mating with self. Self-mating occurs when pollen is transferred between flowers from the same plant or clone, or when flowers self-pollinate. The resulting inbred progeny share many alleles and have a higher degree of homozygous loci than outbred progeny. Repeated selfing or mating among close relatives (such as siblings) results in many homozygous loci and very low heterozygosity. In contrast, the most extreme form of outbreeding is represented by matings between individuals that are unrelated. This is probably only realized in extremely large populations. In most plant populations, the pool of possible mates is limited, and most matings are between individuals related to each other to some degree.

Seed and pollen dispersal distances will greatly affect the relatedness of individuals at different spatial scales and the amount of inbreeding within populations. In general, individuals from distant populations are much less likely to share common ancestors than individuals from the same population or nearby populations. The longer and more isolated populations have been from each other, the more they will have diverged and the less related the different populations.

At what stage do inbreeding and outbreeding play a role in fitness of populations? Once pollen is captured by the stigma of a flower, the success of the pollen in siring seeds is influenced in various ways. First, pollen can be prevented from delivering a sperm cell to the egg cell nucleus within the ovule (fertilization). There are self-incompatibility mechanisms in many plants that prohibit germination of self-pollen, or pollen tube growth in the style, and fertilization is blocked from occurring at all. To understand the inbreeding and outbreeding effects of translocation, it is important to examine what can happen *after* fertilization and formation of a zygote.

The post-fertilization and postzygotic phase of the life cycle is where the various mechanisms come into play that affect the success of the offspring. It is during this postzygotic phase where inbreeding and outbreeding depression, or hybrid vigor or heterosis (discussed below) can be observed. In addition, the effects at different stages of the life-cycle are cumulative. There can be differential success of progeny during seed development and embryo growth, germination, survival to reproductive age, and finally in the ability to produce seed or sire seeds on other plants. Cumulative total fitness of different progeny genotypes can be estimated by multiplying together the proportional success at each of these life-cycle stages. Effects of inbreeding and outbreeding can occur at any or all of these stages.

Effects of mating system on modulating inbreeding and outbreeding: The terms selfing, self-incompatible, and outcrossing are used to describe plant breeding systems, but many plant species, in fact, have a mixture of these systems and there may be diversity in their expression within the same plant, within populations, or among populations. In self-incompatible plants, all the seeds produced by an individual are from pollen of other individuals and are considered completely outcrossed, but there can still be some inbreeding due to mates being related (called biparental inbreeding). In plants that cross-pollinate, but are self-compatible, it is common for at least some seeds to be the result of self-pollination. These individuals are considered to have a mixed mating system (or breeding system) and they usually have intermediate outcrossing rates, depending on the ability of self-pollen to contact stigmas. In self-pollinated plants, all or most of the seeds will be full-sibs, and the outcrossing rate will be low or even 0. About half of flowering plants are self-compatible, and many of those have open flowers pollinated by wind or animals, providing an opportunity for both self and outcross pollen to arrive on stigmas. Overall, it is more realistic to assume a spectrum of possibilities from completely selfing to completely outcrossing, and then estimate where the plant species or population lies on this spectrum, and whether individual or population-level variation in breeding system plays a role. Often, the breeding system of a plant species will be mixed, or intermediate on this spectrum.

Because populations may differ in their rates of outcrossing, the mating system of many species is better represented by a range rather than by a single point. For example, the state flower of Colorado, blue columbine (*Aquilegia caerulea* James), is self compatible and has a mixed mating system, where both selfing and outcrossing frequently occur within a population. It has an intermediate outcrossing rate (t) in the central part of its range in western Colorado (t= 0.469) (Brunet and Eckert 1998, Skaggs et al. 2001). In subsequent studies in Colorado, Utah, and Arizona, the outcrossing rate of populations ranged from 0.59 to 0.85. The rate varied geographically in concert with floral trait variation, plant size, and type of pollinator. Higher outcrossing rates were associated with hawkmoth visitation, lower rates with bee visitation (Brunett and Sweet 2004).

Similarly, when we consider the impacts of artificially induced levels of inbreeding on a plant population, or the effects of outcrossing with a different population, there is a range of possible outcomes based on both species characteristics and environmental features. Context determines the outcome, making it difficult to provide simple rules.

Inbreeding depression: Inbreeding depression is the decrease in growth, survival, or fertility often observed in the progeny that result from matings among relatives. This effect has been demonstrated for many plant and wildlife populations, including numerous species that occur in Region 2 (Table 5.4).

There are two major genetic explanations for inbreeding depression (recently reviewed in Keller and Waller 2002), both of which depend on an increase in homozygosity. The first is that inbreeding depression results from certain deleterious alleles being expressed (because there are now two copies of this allele) which were masked in the more outbred populations by a dominant beneficial allele. The other explanation refers more to the overall diversity of alleles in the plant—the reduction in heterozygosity when plants are selfed or otherwise crossed with close relatives is seen as reducing fitness in general. This latter explanation is based on the concept of heterozygosity being generally advantageous and contributing to fitness, and reductions in heterozygosity—such as that which occurs within inbreeding—will be accompanied by a reduction in fitness.

Inbreeding depression can be measured both within and among populations. In self-compatible species, inbreeding depression can be revealed by comparing the success of progeny resulting from selfed-mating relative to progeny resulting from random outcrossed matings. For species that are obligate outcrossers, more elaborate mating designs compare fitness of offspring related to each other to different degrees. Offspring from matings among full-siblings (share both parents), matings among half-siblings (sibs that share only the mother or father), versus offspring from random matings are compared. Sometimes populations are so inbred that the fitness of random matings within populations is greatly exceeded by crosses made among nearby subpopulations (Keller and Waller 2002). In this case, the increased fitness is gained in the F1 generation and does not return to original low levels after subsequent generations of crossing.

Both within- and among-population inbreeding depression are more likely to occur in small populations than in large populations (because of the relative scarcity of mates), unless there has already been a purging of deleterious alleles following repeated generations of selfing. The severity of inbreeding depression tends to be higher in formerly widespread and outcrossing species than those that naturally experience some level of inbreeding. It is often the result of a cascade of events: populations of plants that were previously connected through pollen or seed exchange become isolated (over long periods of time in nature, or quite quickly as a result of habitat loss or fragmentation that results from human-related activities). They then exhibit higher rates of inbreeding and this leads to more homozygosity. In general, increasing homozygosity also leads to reduced reproduction and survival and ultimately to increased risk of extinction. A study of inbreeding depression in the perennial herb, scarlet gilia (*Ipomopsis aggregata* (Pursh) V. Grant), illustrates the relationship with population size. Seeds were collected from 10 populations in Arizona that differed in size from approximately 12 to 4,500 individuals. Subsequent field studies and pollen transfer experiments revealed that seed size and germination success were significantly reduced in small populations (those with fewer than 100 flowering plants) relative to the larger populations. The pollen transfer experiments confirmed that this was the result of genetic factors (Heschel and Paige 1995). In a restoration context, this could mean that it is preferable to collect from larger rather than smaller source populations, if there are no reasons to suggest otherwise and if both or all candidate populations are presumably genetically appropriate for the project.

Although there is a logical connection between breeding system and susceptibility to inbreeding depression, it is not sufficiently well understood to be entirely predictable. Inbreeding depression is found in many plant species with various reproductive systems and life histories. For example, *Chamerion angustifolium* (L.) Scop., a perennial self-compatible herb, and *Gaillardia pulchella* Foug., an annual self-incompatible herb, are two Region 2 plant species that have been shown to exhibit inbreeding depression (Husband and Schemske 1995, Heywood 1993, respectively).

To the extent that inbreeding depression is caused by unmasking of numerous mildly deleterious alleles, it is possible that continued selfing would eventually lead to their loss or purging from the population. One would then expect a negative relationship between inbreeding (as the plant’s normal breeding system) and inbreeding depression (Holtsford and Ellstrand 1990). This is a useful generalization but doesn’t hold true. In some plants, selfing and inbreeding depression show little correlation when measured at the population level (Johnston and Schoen 1996). This seemingly ironic situation can occur if random genetic drift causes the fixation of mildly deleterious alleles and there is only “between population inbreeding depression”, or when inbreeding depression is so strong that most inbred offspring die in the embryo stage and go undetected (Keller and Waller 2002). Also, given the mixed mating systems of many species (neither purely outcrossing nor purely selfing), this complicates the prediction of inbreeding effects. The relationship between inbreeding and inbreeding depression may depend on additional factors such as the mutation rate to deleterious mutations and the relatedness of the specific mates involved (Affre and Thompson 1999).

Finally, the expression of inbreeding depression may depend on the environment in which the inbreeding occurs. In some studies, inbreeding depression has been much stronger in stressful than in benign environments such as under natural competitive conditions compared to greenhouse conditions (Allard and Hansche 1964, Libby et al. 1981, Dudash 1990, Montalvo 1994). That is, inbreeding depression in some plant species may not be noticed in the nursery, where there are favorable light and moisture conditions. It might not be expressed and noticed until the plants are in the field. Although it is unrealistic to expect information on the likelihood of inbreeding depression in all plant species, any efforts to gain such information or to avoid high-risk situations (such as selfing or crossing close relatives in a highly outcrossing species) might be very worthwhile. In some cases, if it is suspected that a seed collection might exhibit inbreeding depression, one consideration is to sow the seeds directly on site rather than raising the plants in a nursery. Although the latter approach would result in more live plants, it might also allow germination of the more inbred or less fit individuals because of the benign nursery environment. Sowing seeds directly in the field might be more likely to eliminate inbred or poorly adapted individuals before they can contribute to the next generation. These are the recommendations provided for restoration projects involving *Arnica montana* L. (Asteraceaea)—a protected perennial plant species in mountainous regions of central Europe. Significant inbreeding depression for growth rate was observed in plants that were introduced to the field as seedlings (Luijten et al. 2002).

Outbreeding depression: It is obvious that the possibility of inbreeding should be taken into consideration when collecting and translocating seeds for restoration, and that sometimes combining seeds from nearby subpopulations can ward off complications of inbreeding depression. But matings among very genetically differentiated populations can result in the opposite of inbreeding depression—called outbreeding depression. Simply put, this is when the progeny of such a cross have decreased fitness relative to progeny from crosses within the parental populations.

Just as in inbreeding depression, more than one mechanism can cause outbreeding depression. Two main models are implicated in the build up of outbreeding depression (Templeton 1986, Lynch 1991, Waser 1993, Schierup and Christiansen 1996). The first is simply loss or weakening of local adaptation. If each parental population is locally adapted to a different environment, it follows that the hybrid progeny, having only the half the genes of either parent, may be less fit than either parent in their respective environments. Because the environment determines the expression of adaptations, this mechanism is also called the environmental, ecological, or extrinsic mechanism.

The second model involves mechanisms that are intrinsic and environmentally independent in the sense that the relative performance of hybrids and parents is parallel across environments. This can be due to divergence among populations in chromosomal rearrangements or structure and is often reflected in abnormal pairing of chromosomes and in the loss of gamete viability. Though well documented, this mechanism is less common in animals than in plants (Stebbins 1958). Suites of genes that in combination give an advantage to individuals—socalled coadapted gene complexes—may become disassociated through hybridization. This mechanism is also sometimes called the genetic or physiological mechanism.

Outbreeding depression can be the result of either or both of these mechanisms. And there could be additional reasons for outbreeding depression beyond these two, such as unfavorable reactions between two copies of the same gene, different reproductive systems, or transposable elements (Waser et al. 2000).

The amount or severity of outbreeding depression, and how long it persists (over generations) will depend on many factors, including:

a) The breeding system and floral trait variation of the population (both resident and introduced, if they differ). The breeding system can be affected by differences in floral traits and the morphology and behavior of pollinators that service the plants. Differences among populations in timing of flowering also control the opportunity to hybridize.

b) The degree of relatedness of the two parental populations and if they are adapted to different physical environments. For example, in a study of the performance of controlled crosses among six populations of *Lotus scoparius* Nutt.—a subshrub native to California—it was found that overall, the progeny from crosses among the most genetically distant populations (different taxonomic varieties) were only 30 to 50% as fit as the progeny derived from crosses among plants from the same population or same variety (Montalvo and Ellstrand 2001). Up through seed germination, outbreeding depression increased with increasing genetic distance of the crossed populations, indicating a buildup of incompatibilities unrelated to environment. There was also accrual of outbreeding depression during later phases of growth due to a dilution of adaptation, showing that more than one mechanism was responsible for the total outbreeding depression.

c) The environment into which the (hybrid) progeny are introduced. If the environment is different from the parental environments—because it represents a mid-point or transition area between the differing environments of the parents, or because it has been disturbed in some way that happens to be beneficial to the hybrids—then it is possible that the progeny would be as well or better suited than either of their parents to this new environment. If the environment more closely resembles one of the two parental environments, it is less likely that the progeny will be better suited than the resident parent.

d) The fitness of the parental populations. If the parental populations are suffering from inbreeding depression, the hybrids from crosses with certain other populations may show some recovery from inbreeding depression and superiority over their parents. For example, the F1 (first) generation of interpopulation crosses conducted between several populations of partridge pea (*Chamaecrista fasciculata* Michx.) were shown to be almost universally superior to the average fitness of their parents. However, for some pairs of populations, the F3 (third) generation of hybrids (formed from crosses among the F2 progeny) showed loss of fitness relative to the F1s, but still were equal in fitness to their parents. In this case, the context is that partridge pea is a self-compatible, mostly outcrossing species, and these particular parental populations were suffering from inbreeding depression. Thus, the interpretation is that for those pairs of populations, the increased genetic diversity offered by the introduced populations resulted in heterosis that outweighed any potential negative impact from lack of local adaptation (Fenster and Galloway 2000). If the parent populations had not been suffering from inbreeding depression, the results of such crosses may have been quite different.

e) The number of generations hybrids persist and the genetic basis of fitness in the hybrids. When genes at different loci interact, the underlying genetic control of fitness becomes very complex, even when fitness of hybrids is independent of environmental differences. As mentioned in d) above, not all crosses between pairs of partridge pea populations behaved in the same way. The most distantly related pair of populations suffered a drop in fitness in the F3 generation below that of the parental generations. In this case, there was a breakdown in fitness caused by unfavorable gene interactions (epistasis). If there had been a different type of gene action (rather than epistasis) underlying the fitness trait, there could have been a different outcome. The outcome represented true outbreeding depression. This study illustrated the complexity of fitness outcomes and dependence on genetic architecture. In summary, the first hybrid generation of a cross may show one impact (such as outbreeding depression or, alternatively, heterosis), while subsequent generations—either crosses among the first generation hybrids, or backcrosses with one or both parental populations—may show different responses. An example of F1 outbreeding depression and other examples of heterosis in the first hybrid generation followed by breakdown in fitness in the F2 or F3 generation in both plants and animals are reviewed in Hufford and Mazer (2003).

f) Scale of differentiation. The minimum spatial distance between parental plants at which outbreeding depression could arise depends on several factors. These include the spatial scale of gene dispersal (which can be reflected in spatial genetic structure), changes in the environment that affect fitness and the spatial distribution of genotypes, and the strength of selection (Waser et al. 2000). Because of this, one can't reliably determine one constant safe spatial distance for a species over which outbreeding depression would not occur. It could vary between or within populations, and depending on the environment. There are numerous studies that have focused on estimating the physical distance over which outbreeding depression can occur (reviewed in Waser 1993). A series of such studies for the montane herbaceous species *Ipomopsis aggregata* illustrates some of the context dependency of outbreeding depression. One study that compared the fitness of progeny from parents that that were 10 meters apart with that of progeny from parents that were 100 meters apart showed a reduction in lifetime fitness of approximately 30% with the more distant cross (Waser and Price 1989). More sophisticated studies with additional crosses in different years showed that outbreeding depression varied with the environment (Waser et al. 2000).

Other studies have attempted to model more generally the safe or optimal distance for outcrossing, given that some degree of outcrossing could be beneficial (hybrid vigor) and reduce inbreeding depression, but too much is detrimental (outbreeding depression). Most models assume that the genomic incompatibilities that influence fitness of hybrids, such as those seen for partridge pea, will increase with time since divergence of populations. The models rely on having an estimate of how different the populations have become and how long they have been reproductively isolated. Edmands (2002) reviewed the different methods for estimating parental divergence, including geographical, environmental, phenotypic, and genetic distance. One such attempt revealed that the severity of outbreeding depression, in general, is linearly related to genetic distance (basically, the more genetically dissimilar the populations or breeding individuals, the greater the magnitude of outbreeding depression) (Edmands and Timmerman 2003). In addition, outbreeding depression was larger for larger population sizes and lower mutation rates. The duration of outbreeding depression increased with larger populations and with partial self-fertilization. Perhaps most interesting, computer simulations suggested that even small amounts of transfer between populations (the equivalent of one migrant per generation into a population of 100 individuals) could cause as much or more damage as a one-time 50:50 mixture of individuals from different populations. This latter point underscores the gravity of the decisions involved in even very small planting projects.

These issues are relevant to seed collection guidelines for restoration projects. Recommendations of a minimum distance between trees of 300 ft. when doing cone collections and plus tree collections reflect more concern about the possibility of inbreeding than outbreeding depression. The idea is to guard mostly against inbreeding depression and adequately sample the genetic diversity of the tree population. This is a reasonable generalization for many of the commercially significant forest tree species, that are mainly outcrossing, wind-pollinated species. However, these same recommendations, or relative concerns about inbreeding versus outbreeding depression, would not necessarily apply to other plant species with different breeding systems and different susceptibilities to inbreeding or outbreeding depression.

Although outbreeding depression is deserving of concern when moving plant materials between populations, the outcomes from outbreeding are not always negative. There are cases where the advantages of heterosis persist and, as previously mentioned, these are opportunities for longer-term speciation events, or recovery from inbreeding depression. Furthermore, certain hybridizations can be opportunities for a species to expand its range. However, because the result of hybridization is dependent on the inbreeding history and particular genetic architecture that is formed by particular combinations of populations, predicting positive over negative outcomes is exceedingly complex. Second, from the perspective of other species, or biodiversity, natural hybridization zones have other values. For example, although inter-population crosses may result in progeny with less resistance to insect damage, for example (assuming the parental populations have adaptations that relate to different insect species or circumstances), they can also represent zones where insect species or populations are more abundant and diverse. A review of 152 of studies of plant hybrid zones has suggested that hybrids tend to attract or accumulate the taxa of their parent species, and thus become centers of herbivore biological diversity. It was also noted in the review that some species tend to 'prefer' the hybrid zones over the parental species (e.g., in one study more birds were observed nesting in hybrid versus parental cottonwoods, Martinsen and Whitham 1994), and that herbivores are more likely to differentiate among the hybrid classes than they are to differentiate between parental species (Whitham et al. 1999). So, in nature, hybrid zones have other ecological impacts and roles beyond the plants themselves.

In nature, interspecific hybrid zones play important roles in maintaining biodiversity and evolutionary potential. In management regimes, where there is the potential to create such zones at a frequency much higher than would naturally occur and in places and with species and populations that would never naturally meet, there is more risk of doing more harm than good by providing opportunities for hybridization. Conservative practices for restoration, therefore, include avoiding creation of hybrids unless there are well-substantiated reasons for doing so and using seed collections from hybrid zones only for restoration in the same zones unless there are good reasons to use them elsewhere.

Correlations between life history traits and spatial genetic structure

A plant species' breeding system is not the only characteristic that shows some consistent relationships with genetic diversity. A review of genetic data from 449 plant species provided evidence of significant correlations between certain life-history traits and genetic structure (Hamrick and Godt 1990). This review included only studies of allozyme data, and so may not reflect the patterns or relationships associated with other types of genetic diversity or adaptive traits.

General results from this correlation study are presented in Table 5.4. For this study, spatial genetic structure is represented as the strength of the genetic differentiation among populations of a species. The traits are arranged in order of their strength of relationship with spatial genetic structure. Breeding system and life form are most highly correlated with spatial genetic structure. Selfing species and annuals, generally, have stronger genetic differentiation among populations than do outcrossing, wind-pollinated species and long-lived, woody perennial species. In selfing species, approximately 50% of the total genetic variation of the species, on average, is among populations. In contrast, in outcrossing wind-pollinated species less than 10% of the total genetic diversity is among populations. Similarly, the annuals in this study had approximately 36% of their genetic variation among populations, as compared with less than 8% for long-lived woody perennials. To a lesser degree, seed dispersal mechanism, successional status, taxonomic status and regional distribution were also correlated with spatial genetic structure.

The relationships between life history traits and genetic diversity have been more recently explored by the same authors using an expanded dataset (over 700 genetic studies). Their results confirmed the earlier conclusions, with life form and breeding system again showing a high degree of influence on genetic diversity and its distribution (Hamrick and Godt 1996). Exploring combinations of traits, they found that woody plants, in general, have less genetic differentiation among populations than herbaceous plants with the same life-history traits. This was also evident in a representation of the average genetic structure of several plant families, with the families containing mainly woody species having lower genetic differentiation than the others (Table 5.5). The general explanation provided is that the greater height possessed by many woody plant species would allow greater dispersal distance for their seeds and pollen, thereby lowering genetic differences among populations. Observations such as this suggest caution in applying seed transfer zones that have been developed for conifers to other species without additional testing.

An illustration of the impact of breeding system on spatial genetic structure is provided by a group of ten related taxa referred to as the '*Scutellaria angustifolia* complex'. These 10 species and subspecies are herbaceous perennials, occurring in a wide range of different habitats in western North America. They differ in geographic ranges, breeding systems, and other attributes. A genetic study of these plants showed a profound difference in spatial genetic structure that was correlated with breeding system. For example, *S. brittonii* Porter (natural distribution is in Wyoming, Colorado, and New Mexico) is a large-flowered, mainly outcrossing species, and its proportion of genetic diversity among populations was estimated as 0.208. In contrast, S. *angustifolia* Pursh ssp. *micrantha* Olmstead (natural distribution is Oregon, Nevada, and Idaho), a small-flowered, largely selfing subspecies, had an estimated among-population genetic proportion of 0.755. And *S. A. nana* Gray (similar range to ssp. *micrantha*, but also extends into California) is small-flowered but outcrossing and has an among-population proportion of genetic diversity of 0.327 (Olmstead 1990). Thus, although residing within the same genus, the different breeding systems of the three taxa are correlated with very different spatial genetic structure, in a manner consistent with the generalizations of the Hamrick and Godt (1990) studies.

These correlations are, for the most part, reasonable and understandable because of the biological connections between breeding system and gene dispersal systems, in particular, and spatial genetic structure. However, it is important to maintain some skepticism and individually consider the application of these generalizations to each situation for several reasons. First, these generalizations are derived from correlations, not demonstration of cause-effect relationships. Second, they are based on only a small fraction of plant taxa for which there had been genetic studies conducted, and do not provide a reasonable representation for some types of taxa, such as clonal plant species. Third, the study is based entirely on allozyme data and many not reflect other types of genetic diversity. Finally, there is a considerable amount of genetic diversity that was *not* explained by the correlation with life-history characteristics.

These general relationships between life history traits and the spatial genetic structure (SGS) of plants have recently been reinforced with a study of the statistics used to describe fine scale spatial genetic structure and their correlation with such traits (Vekemans and Hardy 2004). They examined studies of SGS in continuous populations of individuals separated by distances of 1 m to 1000 m. The authors quantified SGS with a statistic "*Sp*" that is primarily based on the genetic relationship between individuals, derived this statistic for 47 plant species, and then compared it with several life history characteristics (Table 5.6). For example, the dramatically higher *Sp* value (and hence, SGS) observed in this study for selfing (relative to outcrossing) plant species, is logically explained. First, a high level of inbreeding will greatly increase the rate of genetic drift which has an isolating or differentiating effect among populations. Second, although both pollen and seed dispersal contribute to gene movement in outcrossing species, seed dispersal is the primary agent of gene dispersal for predominately selfing species. So the genes remain more localized, resulting in higher SGS (Vekemans and Hardy 2004).

Landscape considerations

In addition to the evolutionary history and breeding system of species, another important context for interpreting the genetic structure of plants, and the risks of translocation, is their geographic context. The geographic position of populations and the spatial scale over which distinct environmental differences occur can profoundly influence the relatedness of populations over a particular physical distance. This is in part because the underlying heterogeneity of the landscape will drastically influence the occupying vegetation and the spatial scale over which different selective forces play roles in shaping adaptations. The heterogeneity of the landscape with respect to topography, vegetation, moisture, and so on, will also influence the physical continuity or isolation of populations and the ability of pollen and seed dispersal to “glue” populations together. This increases the opportunity for selection and random genetic drift to play roles in population differentiation.

Landscape factors are also critical considerations in situations where the most suitable seed sources are not available for restoration projects. In those cases, clues about the next-best-option can come from considering similarities in the environment between current plant populations and the project site. For example, there was a seed deficit for restoring ponderosa pine on the Boise National Forest (Idaho) after the 1992 Foothills and 1994 Rabbit creek complex fires. The ponderosa pine seedbank had been exhausted following planting after the 1989 fire season. Seed from suitable zones, as identified by seed transfer rules, was very low and these areas also had a history of irregular seed crops. Fortunately, by using a seed transfer expert system (that compared elevation, latitude, and longitude of project site with potential donor sites), Forest Service geneticists were able to identify a suitable seed bank. The introduced material could then act as a palette on which natural selection can act, over time, developing a land race of ponderosa pine that is suited to the Boise National Forest (Mahalovich and Stern 1997).

The probability of finding genetic structure in both adaptive and neutral traits may be higher in geographically and floristically diverse regions such as the Rocky Mountain Range, California, and the Pacific Northwest, than in the more uniform Great Plains. For this reason, the geographic distance of populations may be much less a predictor of genetic divergence of populations in some geographic regions than in others. In areas where heterogeneity is the rule, translocated populations may have a higher risk of experiencing maladaptation and deleterious effects from widely outcrossing. When considering the probability of translocations causing maladaptation, outbreeding depression, or genetic rescue from inbreeding depression, we would do well to consider these factors. As briefly reviewed here, the historical patterns of plant migrations from refugia following glaciation influences the genetic structure of populations. As will be noted in Chapter 6, this history can sometimes be more important to consider in the estimation of risk than actual spatial distance of populations.

Table 5.1. Contrasts and comparisons among various DNA markers that can be useful in genetic monitoring (modified from Gillet 1999). Note: developed in the context of plant species. Does not apply completely to animal genomes or systems.

	Mode of inheritance				
Marker type	**Mode of transmission**	**Mode of gene action**	**Level of genetic variability**	**Function**	**Primary application**
AFLP fingerprint	biparental nuclear, many loci, unknown number of alleles per locus	dominance at some loci, codominance at others	hypervariable, i.e., each individual has unique banding pattern	unknown	pedigrees
Nuclear microsatellites	biparental nuclear, few loci, many alleles per locus	codominance, with exception of null alleles at some loci	large variation within populations, low differentiation between population	non-coding, may contribute to genome stability	gene dispersal over small spatial scale, small-scale structure, paternity analysis, pedigrees
Chloroplast microsatellites	uniparental (maternal in angiosperms, paternal in conifers), pseudo-haploid, single locus, many alleles per locus	each cytotype is expressed	low variation within populations, large differentiation between populations	non-coding	Small-scale structure, diversity, differential dispersal by pollen and seeds, phylogeography
Chloroplast DNA (cpDNA) (using RFLP)	uniparental (maternal in angiosperms, paternal in conifers), haploid (but many copies/cell), one or more loci, many alleles per locus	each cytotype is expressed	low variation within populations, large differentiation between populations	coding (functional differences possible among alleles at locus) and non-coding	phylogenies, differential dispersal of seeds and pollen, phylogeography, hybridization
Mitochondrial intron marker	uniparental (maternal in most plants) pseudo-haploid, single locus, many alleles per locus	each cytotype is expressed	low variation within populations, large differentiation between regions	non-coding	phylogenies, differential dispersal of seeds and pollen, small scale phylogeography
Mitochondrial DNA (mtDNA)	uniparental (maternal in most plants), pseudo-haploid, single locus, many alleles per locus	each cytotype is expressed	low variation within populations, large differentiation between regions	coding (functional differences possible among alleles at locus) and non-coding	phylogenies, differential dispersal of seeds and pollen, large scale phylogeography, hybridization

Table 5.1. Continued.

	Mode of inheritance				
Marker type	**Mode of transmission**	**Mode of gene action**	**Level of genetic variability**	**Function**	**Primary application**
ITS of ribosomal DNA	biparental nuclear, several loci, several alleles per locus	codominance	high variability, even within a single individual	non-coding	phylogenetics, systematics
cDNA markers	biparental nuclear, one to a few loci, few alleles per locus	codominance	low variation within populations, low differentiation between populations	functional differences possible between alleles of a locus	phylogenetics, systematics
Isozymes and allozymes	biparental, nuclear, 1-5 loci, 1-7 alleles (allozymes) per locus	codominance	low to medium variation within populations, low differentiation between populations	functional differences possible between alleles of a locus	population structure, genetic distance, genetic diversity, historical gene flow, paternity analysis (limited), hybridization

Table 5.2. Groups of species in the Great Plains and Intermountain West floras with high frequencies of hybridization and no reported hybridization (from Ellstrand et al. 1996).

Six families and four[1] genera with the most hybrids				Five largest families with no reported hybrids in floras examined		
Families	**Hybrids**	**Genera**	**Hybrids**	**Families**	**Genera**	**Species**
Great Plains flora (171 families, 855 genera, 2,778 species)						
Asteraceae	29	*Aster*	10	Cyperaceae	13	113
Poaceae	20			Brassicaceae	36	99
Rosaceae	15	*Rosa*	9	Ranunculaceae	12	53
Fabaceae	14			Apiaceae	31	52
Amaranthaceae	13	*Amaranthus*	12	Caryophyllaceae	17	50
Verbenaceae	8	*Verbena*	8			
Intermountain West flora (64 families, 492 genera, 2,316 species)						
Asteraceae	43			Liliaceae	23	60
Scrophulariaceae	19	*Penstemon*	10	Lamiaceae	24	45
		Castilleja	7			
Poaceae	19	*Stipa*	7	Solanaceae	9	32
		Oryzopsis	7			
Cyperaceae	11	*Carex*	9	Asclepiadaceae	4	21
Boraginaceae	7			Rubiaceae	4	14
Orchidaceae	6					

[1] In one case, five genera are listed because of a tie.

Table 5.3. Evidence of cytoplasmic (cpDNA) genomic capture in plant species. Examples here are presumably a result of either recent or historical hybridization between related species (adapted from Avise 2004).

Genus	Common name	Reference
Argyroxiphium	Silverswords	Baldwin et al. 1990
Helianthus	Sunflowers	Rieseberg et al. 1990b
Heuchera	Heucheras	Soltis et al. 1991; Soltis and Kuzoff 1995
Pinus	Pines	Latta and Mitton 1999
Populus	Poplars	Smith and Sytsma 1990; Martinsen et al. 2001
Quercus	Oaks	Whittemore and Schaal 1991; Dumolin-Lapegue et al. 1999a
Salix	Willows	Brunsfeld et al. 1992
Zea	Teosintes, maize	Doebley 1989

Table 5.4. Correlates between life-history traits and spatial genetic structure (differences among populations) in plant species. Derived from Hamrick and Godt 1990. Traits are ordered from highest to lowest correlation with spatial genetic structure.

	Correlation with spatial genetic structure	
Trait	**Highest**	**Lowest**
Breeding system	Selfing species	Outcrossing, wind-pollinated species
Life form	Annual	Long-lived, woody perennial
Seed dispersal mechanism	Gravity	Gravity and animal-attached[1]
Successional status	Early	Late
Taxonomic status	Dicots	Gymnosperms
Regional distribution	Temperate	Boreal-temperate

[1] This is one mechanism: seeds fall from plant by gravity and are then dispersed by animals.

Table 5.5. Average levels of among-population genetic differentiation (spatial genetic structure) for several plant families (adapted from Hamrick and Godt 1996).

Family	**Number of species studied**	**G_{ST} (among-population genetic differentiation)**
Chenopodiaceae	22	0.540
Solanceae	23	0.426
Cucurbitaceae	23	0.397
Schrophulariaceae	16	0.372
Onagraceae	23	0.338
Poaceae	91	0.284
Fabaceae	48	0.277
Asteraceae	101	0.204
Myrtaceae*	14	0.134
Orchidaceae	16	0.087
Fagaceae*	27	0.085
Pinaceae*	103	0.073

*Families with predominantly woody taxa.

Table 5.6. Effect of life-history characteristics of plant species on the '*Sp* statistic' measuring spatial genetic structure (SGS) (from Vekemans and Hardy 2004). The higher the value of the *Sp* statistic, the more likely individuals that are physically close to one another are also related to one another. The studies included in this survey were continuous populations and data were collected over relatively short distances (less than 1000 m).

Effect[1]	**Number of species in analysis**	***Sp* statistic (mean)**
*Breeding system**		
Selfing	5	0.1431
Mixed mating	7	0.0372
Outcrossing	18	0.0126
Self-incompatible	17	0.0134
*Life form**		
Herbaceous	24	0.0459
Small trees	6	0.0259
Trees	17	0.0102
Pollen dispersal		
Animal-dispersed	17	0.0171
Wind-dispersed	6	0.0064
Seed dispersal		
Gravity-dispersed	6	0.0281
Wind-dispersed	5	0.0120
Animal-dispersed	8	0.0088

[1] *Sp* values that are statistically different ($P<0.01$) from one another, within a trait category, are indicated with an asterisk beside the trait.

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Chapter 6

What is Genetically Local?

If a plant is “genetically local” to a site, it would be adapted to the site and compatible with existing populations of the same species. In addition, all of the reasons outlined in Chapter 1 for choosing genetically appropriate plant materials for revegetation projects would likely be satisfied if genetically local populations were used. That said, a consensus definition of the term is elusive and depends on whether or not one considers just the introduced plants, the population residing at the site, interacting populations of other species, or all of these categories of populations.

A simplified definition of genetically local plants (see Glossary) is: “plant materials that reflect the amount and type of genetic diversity that is typical for a particular plant species in the area under consideration.”

The interpretation of genetically local appears to differ among disciplines. In forestry and agronomy, the term takes on a more limited meaning than in the statement above. The focus is on the probability of planted genotypes *not* being maladapted and therefore not experiencing a loss of fitness relative to the resident population. For example, seed transfer research in forestry tends to focus on growth rate, cold hardiness, disease resistance, and mortality of introduced material relative to the local population. In the context of plant community-level biodiversity, the concern is whether there is a change in fitness of the planted population, the resident population, or other populations with which the introduced plants interact, relative to the introduction of local genotypes. In ecological and population genetic modeling, changes in fitness can be quantified as an increase or decrease in numbers of individuals over time. If in a modeling exercise, the population eventually goes to zero, it is said to have gone extinct (in rare species conservation, such local extinction is called extirpation). These models evaluate the risk of population extinction and allow ecologists and population geneticists to mathematically estimate various types of effects on the fitness of populations, including effects of adding genotypes that differ from those present in the local population.

In each of the above contexts, the decline in fitness and possible local extinction could take many generations, resulting in a gradual decline in reproductive success and numbers of individuals. In contrast, the decline could be rapid if the introduced genotypes lack critical local adaptations. For example, seeds may fail to germinate or flowers may fail to initiate under prevailing day length and temperature combinations. More often, the decline is gradual, and involves the introduced population, resident population, or both. For example, if introduced genotypes have antagonistic interactions with resident genotypes such that hybridization results in outbreeding depression, or out of phase flowers unsuccessfully compete for pollinators, extinction risk can increase for one or more population.

How can one determine if introduced genotypes are likely to raise or lower the fitness of populations and alter extinction risk? How can it be determined if the effects are due to adaptive differences, genetic incompatibilities that show up after cross-pollination, the beneficial effects of added genotypes, or something else? There is a treasure chest of research tools available to estimate where germplasm can be collected and deployed while staying below a significant level of risk. Common garden and molecular marker studies provide the data for making estimates. These data are sometimes used to model the increase or decrease of translocated populations (growth or extinction trajectories). Many current germplasm transfer guidelines for single tree species (henceforth referred to as seed transfer guidelines) make use of such data to set limits for collection and distribution of germplasm.

This chapter aims to provide the Reader with a better understanding of translocation risk. While Chapters 4-5 provide the basics of genetic concepts important to making genetically appropriate decisions, this chapter describes some of the research methods that examine impacts of translocation on population fitness. It also shows how some researchers quantify risk without getting into the detailed statistical models they use for data analysis. In this chapter, we will examine:

- The meaning of adaptation
- Historical context of “seed transfer zones” and “seed transfer guidelines” in forestry
- Methods that identify and quantify risk of translocation (common gardens)
- Studies that examine the potential for hybridization and effects of hybridization.
- The value of molecular marker studies in prediction of risk patterns
- Translocation and species interactions
- The magnitude of population differentiation and estimates of translocation risk
- Ecological genetic models that aid understanding risk of translocation

Detailed description of the analytical methods used to quantify risk for construction of seed transfer guidelines is not covered here. Other publications describe procedures and statistical tools used to evaluate risk from experimental data (for example, Rehfeldt 1988, 1991, 1995; Sorensen et al. 1990; Campbell 1991, 1992; Westfall 1992). A recent review (Johnson et al. 2004) describes research used to develop continuous seed transfer guidelines for trees to illustrate how these tools might be used for other species.

Once risk is quantified or estimated based on knowledge about the biology of the species (see Chapters 9-11), decisions can be made about what constitutes an acceptable level of risk. Political and social concerns do not enter the quantification of extinction risk, but they can enter administrative decisions as to what is *acceptable* extinction risk under different management contexts. “Acceptable risk” may be modified, for example, to balance projections about short versus long-term multiple uses of National Forests and how some uses might usurp others. It might also include estimates of the financial cost of using genetically local plant materials, weighed against long-term financial costs and estimated impacts of non-local genotypes on native biodiversity (the extinction risk cost). Other costs could include, for example, loss human life and property or increased colonization by invasive species if there is no planting, adverse effects on wildlife, feasibility, and the relative effects of translocated genotypes. This type of exercise is not within the scope of this Guide.

Adaptation

Readers, since childhood, will be familiar with the term "adaptation." It is used in numerous contexts and has various meanings. In this Guide, we are of course referring only to biological adaptation, which is one of the core concepts to understanding the question, "what is genetically local?" For this reason, a careful understanding of the term is important. The meaning of adaptation was carefully reviewed and framed by George C. Williams (1960) in his classic book *Adaptation and Natural Selection*. Another recent book, *Adaptation,* devotes 500 pages of text to the historical and modern usage of the concept (Rose and Lauder 1996). In these scholarly works, it is made very clear that the concepts surrounding the term have evolved with the accumulation of new information and scientific progress. An impressive amount of semantic debate has accumulated about correct usage. In this Guide, we use a working definition of the terms "adaptation" and "adapted" consistent with mainstream use in modern evolutionary biology.

The term adaptation refers to both the process of a trait becoming modified over time so that it becomes better suited to the surrounding environment, as well as to the product of the process. We define the process of adaptation as repeating cycles of reproduction and selection such that, over time, traits better suited to the environment increase in relative frequency or intensity. This assumes the traits being modified are genetically determined and genetically variable. Adaptation occurs over time and acts at the level of the population, not the individual. The new trait structure or function resulting from natural selection is referred to as an adaptation. If an organism possesses adaptations to the current environment, it will be adapted to its current environment. For example, a high elevation genotype that flushes leaves late in the season and grows fast in a time window that is appropriate for a short growing season possesses an adaptation that allows it to do well at high elevation. However, if the genotype is moved to a much lower elevation where other genotypes that flush leaves much earlier have a higher survival and reproductive rate than the plants with late leaf-flush, it would be considered maladapted. In addition, if the low elevation genotypes that flush leaves early move to high elevation, they could suffer extreme frost damage. Other classic differences would be shorter stature of high elevation genotypes. This might not be a problem at lower elevation, but if high stature genotypes are moved up, there may be top breakage from snow loads. In this chapter, we examine how to determine if populations are differently adapted.

"Seed transfer zones" and "seed transfer guidelines" and reducing risk

The field of forestry has added greatly to the understanding of genetic principles important to restoration, methods for determining local adaptation, and analyses that are useful for establishing seed transfer guidelines for restoration purposes. Nearly every forester, biologist, and natural resource manager on National Forests and Grasslands will be familiar with seed transfer zones that are used when species specific data are unavailable to guide seed transfer of trees. For example, in Region 2, generalized seed zone maps by Cunningham (1975) are used to guide seed collection and distribution of trees and shrubs in the absence of species specific guidelines (Seed Handbook, USDA Forest Service 1993, 2004 in prep.). In Chapter 9 of this guide, Figures 9.1-9.3 show the generalized seed zone maps for Colorado, South Dakota, and Wyoming. The Seed Handbook defines "seed collection zone" as:

> "*Area having defined boundaries and altitudinal limits within which soil and climate are sufficiently uniform to indicate high probability for maintaining a single subdivision of plants that are adapted to a specific set of environmental conditions. Geographic subdivisions within a region encompassing areas of similar environmental conditions; boundaries between subdivisions may or may not be based on patterns of genetic variation for adapted traits. Seed zones are two-dimensional in scope, based on a geographic boundary (latitude and longitude), sometimes modified by guidelines for minimum and maximum elevations within the zone.*" (FSH 2409.26f zero code)

Though helpful, this is not the optimal solution for guiding seed deployment. Ideally, seed transfer guidelines for all major revegetation species, including shrubs, forbs, and grasses, would be based on actual research that identifies adaptation, ecological roles, and extinction risk of planted species and interacting species. This would be a great improvement over use of generalized mapped boundaries based solely on climate, soils, and other physical factors on a coarse grained (rather than fine-grained) scale. The Seed Handbook recognizes that genetic data can help to modify fixed seed zones. The quote above continues on to say:

> "*When genetic data become available for individual species, most of the patterns of adaptation are related to zones of equal hardiness. Generally, there are no guarantees of minimizing adverse genotype-by-environment interactions within a zone, as seed sources within a zone have not been tested across a range of environments.*" (FSH 2409.26f zero code)

More detailed guidelines advise on a species by species basis, where germplasm can be collected and deployed with minimal overall risk. For some of these, genetically local areas will have identifiable geographic areas associated with steep rises in risk, but often they will not conform to simple lines on a map. Risk patterns can be complex and depend on species attributes, geographic location, migration history, and habitat complexity. Each species is different, but groups of species may be similar enough to share some generalized guidelines.

Provenance tests and seed transfer in forestry. Research comparing tree provenances (accessions from distinct populations) in multiple locations began in the middle of the 18th Century in Europe and was well established by the middle of the 20th Century in many parts of the world (Callaham 1964, Langlet 1971). Seed transfer guidelines aided by the results of provenance research have been devised throughout the US, Europe, and many other countries throughout the world. Originally, guidelines were established to increase the production of timber products and for tree improvement, not for ecological restoration of forested land (Lacaze 1978). As the principle of multi-use became more engrained, plantings within National Forests of the US shifted toward a more restoration-oriented goal.

Because timber trees generally take a many years to reach harvest size, knowledge of the source of seeds and the limits to their success when planted in different areas has been of utmost importance. This is true whether the goal is restoration or timber production. However, in tree improvement programs, seed collection zones have not always coincided with the geography of seed deployment (Westfall 1992). Within the US Forest Service, the planting of tree orchards for harvest has always included a goal of long-term population persistence and diversity of genotypes, but not necessarily natural biodiversity of plant communities. Tree seeds have sometimes been planted far from source sites, even on different continents, as long as the environment was suitable. Currently, the National Forest System does not target harvest productivity. Instead, the target is natural biodiversity and increased forest health. However, when devising seed transfer guidelines for non-tree species in the context of restoration, it is useful to recognize the older tree production context when applying seed transfer concepts. Seed transfer guidelines for all types of plants and contexts hold in common—whether the goal is harvest within 50 years, long-term population persistence, overall biodiversity, or all of these—the concept of minimizing extinction risk through maladaptation.

State and Federal agencies in the US have long recognized the value of using local sources of seeds for reforestation and began constructing seed transfer guidelines in the form of seed zones in the 1930s (McCall 1939, Schubert et al. 1971). The earliest tree seed zone maps in the western US were constructed using general ecological concepts to guide seed transfers in the absence of experimental data. The maps were spurred on by a long history of provenance tests that showed large differences in performance of seed accessions grown in different environments. The zones were drawn as distinct areas on a map using a variety of geographic, elevation, geological, and climatic zone data. For the Great Plains (including much of Region 2), Cunningham (1975) published a provisional seed zone map for collection of tree and shrub seeds. He overlaid isopleths (=isograms) in precipitation and temperature (in particular winter lows) onto Major Land Resource Regions (which partition the landscape into regions based on dryland crop evapotranspiration) to identify areas of shared physical environment. He then altered some zones based on political boundaries and geographic features. As such, seed collection zones have traditionally had rigid boundaries superimposed by elevation subzones to provide appropriate adaptive choices for seed transfer.

When provenance trial or other data on seed transfer become available for a species, species-specific seed zones can be constructed (see Figures 6.1 and 6.2—discussed later for revised seed zones for ponderosa pin). These can differ greatly from the generalized seed zones of Cunningham. It is also possible to devise continuous seed transfer (incorporated into Forest Service Seed Handbooks). Continuous seed transfer guidelines go beyond the concept of mapped boundaries. They recommend the distance seed can be transferred from a particular point of origin, both geographically and within a range of elevations, while describing the relative risk associated with that transfer (Johnson et al. 2004). In forestry this relative risk has been traditionally based on risk of maladaptation defined by statistical analysis of provenance test data (see below).

Extending beyond the forestry model. Many tree species for which detailed seed transfer guidelines and seed zones have been constructed are highly outcrossing conifers with wind-dispersed pollen and single ploidy levels. There are notable exceptions that do not fit this mold, but for the majority, gene flow tends to be substantial and population structure tends to be very clinal as opposed to ecotypic (Chapter 5). Adaptive differences are often evident upon planting in distant locations or elevations that differ in physical conditions. Because many conifers have high levels of gene flow, the risk of maladaptation from transferring seeds beyond the criteria set in seed transfer guidelines, is thought to be much more important than potential outbreeding depression. Also, risk of inbreeding depression tends to be higher than for outbreeding depression. The assumption of generally low outbreeding depression, though logical, has not really been tested. Tree improvement researchers have used wide crosses (mostly between species) to look for heterotic F1 progeny for production. Heterosis was often found for particular crosses with respect tree production traits, but F2 and back crosses have less often been checked for hybrid breakdown. In wide crosses in Douglas-fir, some had good performance. The least successful cross was between very distant British Columbia and California trees (Orr-Ewing 1966). For many other plants, especially those with mixed mating systems, the risk of outbreeding depression (Chapter 5, 7) may be more substantial. For this reason, when applied to plants in general, it is useful to expand the definition of seed transfer guidelines to include this second arena of risk. Others have defined seed transfer "zones" (meaning guidelines) more generally as:

> "*geographical regions within which individuals (seeds, seedlings, or adults) of native species can be transferred with no detrimental effects on population mean fitness*" (Hufford and Mazer 2003).

This definition does not tie lowered fitness to a particular mechanism. It describes seed transfer zones as areas within which native plant materials can be moved with minimal risk of fitness loss from any mechanism, including maladaptation, inbreeding depression, and outbreeding depression. The areas need not have distinct boundaries. Instead, they are continuous and represent areas of probability associated with risk of lower performance than would occur by moving populations only within seed and pollen dispersal distances of targeted planting sites.

Experimental research approaches that inform seed transfer guidelines

By far, the most common data in the construction of seed transfer guidelines (in contrast to zones) are from experimental studies that identify adaptive differences among populations. In Chapter 4, we mentioned that common garden studies can be used to identify the relative influences of the genotype and the environment on phenotypes. We also mentioned how they can be used to detect the amount of variation in a quantitative trait (including fitness components such as survival and seed production) due to differences among individuals of the same population relative to differences among populations. Furthermore, by placing samples from more than one population in common gardens in more than one environment over a species' range, it is possible to reveal differences in survival, growth, and reproduction among populations in contrasting environments. In addition to revealing if there are significant differences in adaptation, the risk of maladaptation can be quantified from these data. To estimate the additional risk of outbreeding depression, hybrid progeny performance can be evaluated in common gardens alongside samples from parental populations. Below we describe the basic common garden study and extensions of these basic studies. All can be used for tree and non-tree species. As such, the discussion is generalized to include all seed plants.

Common gardens. Common garden studies are experiments that involve the planting of different individuals in a common environment so that genetic differences among individuals can be revealed. This allows one to ask questions about population structure, differential growth, inheritance of traits, or effects of multiple environments. One of the major assumptions in a common garden study is that environmentally induced variation in genotypes (phenotypic plasticity) is diluted by the sharing of a common growing environment. Natural environments are heterogeneous, so it is expected that some of the variation observed among individuals or populations *in situ* is caused by environmental rather than inherited genetic effects. Carefully designed and executed common garden studies can determine how much of the variation in phenotypes is caused by genetic differences and how that variation is structured. The way a common garden is designed (for example the level of relatedness among seeds, growth stage planted, and uniformity of the garden environment, amount of replication) can make a big difference in the ability to detect heritable genetic variation.

Many common garden studies have been planted with clonal replicates of multiple individuals, sometimes in contrasting environments, but most have been planted with seeds collected from one or a few wild populations. If seeds collected from the same mother (maternal sibship) are tracked within an experiment, then progeny of different families can be compared in a "progeny test." When using wild-collected seeds, the seeds from a particular mother plant can be full-siblings (sharing the same mother *and* father), they can be half-siblings (sharing the same mother but having variable fathers), a mixture of full- and half-siblings, or the result of self-pollination (selfed full-siblings), depending on the plant's breeding system. Knowledge of the mating system (the amount of cross pollination) helps in identifying the proper genetic model for analyzing the data so that the amount of genetic variation can be appropriately estimated.

If only the mother can be identified in the family structure, then the estimates of additive genetic variation (the variation that can respond to selection) will be confounded with maternal effects and non-additive genetic variation. This bigger, confounded term is known as broad-sense heritability. Additive and non-additive genetic variation and maternal effects, which tend to be negligent in mature woody plants, can only be identified separately if both parents can be identified. In conifers, the identity of mothers and fathers and if siblings are full or half, can be figured out by genotyping the embryo and the part of the seed derived from the mother's tissues. In flowering plants, such identification usually requires use of a controlled crossing design, which is a lot more work than using open-pollinated seeds. In either case, the most accurate designs use progeny derived from hand-crossing parents so that all major components of genetic variance can be determined (Lynch and Walsh 1998). If the test is planted on more than one site, we can then discern how much of the total variation is attributed to the environment versus possible genetic effects and reveal differences due to source population, families, garden test site, and interaction effects, including genotype-by-environment interactions (G x E). If more than two sites are used, the form and significance of any G x E can be determined.

The relatedness of the progeny in a family will affect how much of the variation in a measured trait is explained by differences among the hierarchical levels represented in the experiment (within family, among families within populations, among populations). This allows one to estimate how much variation in the phenotype is due to differences in the environment relative to genotypes. In addition, these hierarchical components of variance can be used to estimate population structure based on quantitative traits (see Q_{ST}, Chapter 4).

Certain factors can bias the variance attributed to differences among families and populations. Non-additive effects (dominance and epistasis) can be expressed at any stage of the life cycle and can be a significant part of fitness. Also notable are "maternal effects," especially during germination and seedling growth (Roach and Wulf 1987; Shaw and Byers 1998). Most maternal effects are caused by environmental influences on plants while seeds are maturing. Size, quality, and germination behavior of resulting seeds often display maternal effects that tend to be confounded with genetic differences. Some traits are affected by the environment of the mother, for example the amount of carbohydrate allocated to the developing seeds. This could affect the germination time or size of the seedling due to the nutrient status of the mother. Such maternal effects could inflate the difference among families—or populations. Maternal effects can sometimes influence more than one generation and can occur in annuals or perennials, but effects tend to dissipate with age, becoming small as a plant reaches maturity (Montalvo and Shaw 1994, Shaw and Byers 1998).

Common garden studies can be short- or long-term, in single or in multiple locations. Most are short-term, including most studies done for designation of tree seed transfer. In general, all kinds of common garden studies are valuable for finding adaptive differences and trends among populations and for making qualified decisions about plant translocations.

Common gardens in multiple environments (provenance tests) and detection of local adaptation. Common garden studies that use multiple accessions from diverse source locations (usually bulking individuals from particular accessions as provenances) are also known as provenance tests. These can be replicated across multiple environments to test for differences among accessions in adaptation to the different test environments. The source populations and test locations ideally span the geographic range of the species, but often they span the range of habitat variation within a geographic region of interest. Plantings are ideally reciprocal such that every accession is planted at every test location, but this is time consumptive and expensive to do. Various measurements are recorded over time, including traits that are known or suspected to affect the success of the species in particular habitats. In addition, if traits that represent components of population fitness (germination, survival, seed and pollen production) and traits that affect fitness (cold hardiness, resistance to herbivores) are measured, it is possible to examine the fitness effects of translocation to specific environments and how particular phenotypic traits correlate with fitness. Howe et al. (2003) describe how studies of quantitative traits have often revealed population differentiation for traits associated with adaptation to cold and cold hardiness. Such studies have shown that the timing of bud flush is a major adaptive trait because it allows avoidance of frost injury. Translocation outside of adaptive zones often has a high risk of cold injury, such as when moving plants from lower elevations upward or from southern latitudes northward.

Based on quantitative genetic models, significant differences among seed accessions or clonal replicates imply there are genetic differences among populations that are heritable (design determines if broad or narrow sense heritability). Broad sense heritability can be estimated from accessions that bulked seeds from different families or if fathers are unknown. Narrow sense heritability can be estimated if the parents of all progeny are known. If populations perform differently in different test environments in a parallel way, that is, they all have the same ranked performance in each test environment, this means that all are adapted to the same conditions, but some are better adapted than others. In contrast, some populations may do better than others only in *certain* environments. Statistical analysis, notably analysis of variance (ANOVA), can quantify these different kinds of effects. In both examples, the ANOVA would show significant effects of seed source and planting location. In the later case, the ANOVA would also show a significant population-by-environment interaction (G x E) which, put simply, says that one population does better in one environment and the other does better in the other environment.

The most simple design for detecting this type of local adaptation involves two populations grown together in just two environments. If the environments are the reciprocal *native* environments, this test is called a reciprocal transplant study. If the populations show significant differences in phenotypes and performance in the common gardens, it is assumed that these differences are at least partially genetically determined. When the two test populations each do best (attain higher fitness) under their resident site conditions, the populations are considered locally adapted to their home test site and maladapted to the foreign test site.

As explained in Chapters 4-5, genetic differentiation of populations can occur by any combination of evolutionary processes, including natural selection, non-random mating, genetic drift, and migration. Thus, not every population is expected to be optimally adapted to its home environment. For this reason, comparing just two populations reduces the ability to detect differences in local adaptation. Provenance tests comparing many populations are more likely to detect patterns in local adaptation, as well as patterns of range-wide differences in adaptation. The analysis becomes more complex when more than two source populations are included in the study. Significant source population-by-environment interactions still indicate differences among populations in adaptation, but the interaction, *per se*, does not indicate *local* adaptation. It is necessary to examine the relative fitness of the populations in each environment to see if the home population, on average, has the highest fitness. It is also useful to examine if the rise and fall of fitness is associated with particular morphological traits. In addition, one can ask if there are potentially functional associations between traits associated with fitness and potentially influential environmental conditions at the source location (such as first date of frost or average precipitation).

Provenance studies with trees in multiple environments have been performed for over two centuries in Europe (Langlet 1971), and since the early 1900s in this country. The best known studies outside of forestry were those by the Carniegie Institute in California in the 1930s (Clausen, Keck, and Hiesey 1940) and by Turesson in Europe before 1920 (Turesson 1922). The California studies involved many species of herbaceous perennials that could be propagated vegetatively to allow testing of genotypes across multiple environments. A main goal of these later two bodies of work was to understand the natural distribution of plants and their phenotypes. They looked for differences in adaptation and if the source environment affected survival, reproduction, and the distribution of phenotypes. In these studies, plants from many different habitats were grown together in reciprocal locations, exposing patterns of variation that were attributed to differential adaptation to the large environmental differences. The studies identified “ecotypes” but as Johnson et al. (2004) point out with regard to the Carniegie studies, the limited number of populations may have precluded detection of more continuous variation as in clines or stepped clines. The studies were a landmark and showed many obvious patterns in adaptation to the environment. These early experiments were designed when statistical methods for analysis were relatively new, so statistical analysis was limited. But they set the stage for many further experiments by ecologists, systematists, and population geneticists.

The tradition of common gardens is also used in agronomy to test native plant materials under development before they are released to the public (Chapter 8). They test multiple accessions to determine which ones perform best under particular circumstances, based on particular desirable traits and goals (such as forage quality, turf formation, rapid establishment, or tolerance of mine site conditions). The accessions with the desired attributes for particular purposes are then selected for further development. Vogel et al. (2004) described the importance of knowing the adaptation of each intended restoration species to particular sites or regions, especially for plant materials designated for various kinds of revegetation projects. The authors suggest combining available ecoregion and hardiness zone classification systems to develop “Plant Adaptation Regions” (PAR’s). They provide examples of creating these new maps.

Duration of common garden experiments. Long-term provenance trials test accessions over multiple, usually environmentally-contrasting locations for many years. The longer the term of the trial, the more likely the experimental populations will be affected by sporadic environmental events. These sporadic events can be highly influential in shaping the evolutionary history and current genetic composition of the study populations. Johnson et al. (2004) emphasize in their review that long-term trials have revealed that although many populations can perform well during average climatic conditions, many non-local accessions could not tolerate the rare events survived by local populations. For example, in a study with ponderosa pine (*Pinus ponderosa*) in California, after 12 years there were obvious trends related to the elevation of seed origin. Low elevation populations, however, were growing faster than high elevation populations at a high elevation site. By year 29 the high elevation populations outperformed low elevation populations (Conkle 1973). Johnson et al. (2004) provide an example for a Douglas-fir (*Pseudotsuga menziesii)* trial in which it took 30 years before severe weather caused much more serious damage to off-site seed sources than local sources. Other kinds of sporadic events may also be geographically restricted such as drought, disease, changes in pollinator populations, and insect outbreaks. Long-term studies are especially important for species that take many years to reach reproductive maturity.

The duration of experiments needed to determine fitness differences will depend on the life-form and life history of the plant species. Trees, long-lived shrubs, and herbaceous perennial species can have large differences in generation time. The longer it takes to reach reproductive maturity, the longer it takes to measure fitness components such as number of seeds produced or seeds sired. Annuals and short-lived perennials can be measured over their entire lifetimes to obtain measures of lifetime fitness (up to one year in an annual and two or more years in a perennial). Significant G x E (local adaptation) may not show up in studies of short-lived plants unless studies are replicated over a number of years.

Using common garden results to quantify translocation risk. Forest geneticists often assign levels of risk (in this case planting failure or productivity loss) based on associations between environmental variables and plant traits. Although not specifically designed for it, the concept can be useful in restoration. They usually measure variation in traits that have been found to affect fitness. An important underlying assumption is that a significant association between a trait (for example time of bud flush) with an environment variables (for example longitude, latitude, elevation, annual precipitation) is caused by adaptive differences among populations. Johnson et al. (2004) listed seven steps for analysis of common garden test data. First, designate a sample range—this may be an administrative area or natural region. Second, collect seed from many diverse sites distributed over the sample range, keeping seed samples separated by maternal parent. Third, plant the maternal families randomly within common gardens in one or several locations within the sample region. Fourth, measure traits suspected to have adaptive significance, traits associated with reproductive success, and other components of fitness as possible. Fifth, run a statistical analysis to determine which traits differ significantly among seed sources. Sixth, for traits that differ, run a regression analysis to find any functional associations between the traits and physical environmental variables such as climatic gradients, elevation, latitude, and longitude associated with the collection location of each source population. Finally, determine for each variable how much overlap exists among population sources along an environmental gradient. The degree of overlap determines translocation risk among regions. The higher the overlap the lower the risk of maladaptation. Rehfeldt (1991) suggests using a least significant difference of 20% (0.8 probability of being different) to guard against accepting that there are no differences among populations when differences actually exist. The least significant difference is the minimum amount of difference between any pair of means that is statistically different.

Within any identified geographic region, the slope of the decline in fitness (or change in a phenotypic trait of adaptive significance) in relation to environmental parameter(s) also quantifies the risk of translocation. For example, in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), as the elevation of the source populations increased, growth potential decreased. The steepness of the decline in trait value (growth potential in this instance) and the shape of the geographic cline, quantifies the risk. The least significant difference defines differentiated populations along the environmental gradient (elevation in this instance). The regression predicted that within a particular geographic area, deployment of seeds beyond about 400 m in elevation would result in a significant decrease in height after four years of growth, relative to planting at the home site elevation. Likewise, deployment of source populations among some geographic regions was predicted to result in significant risk of maladaptation— for example, between the San Juan Mountains of CO and Dixie or the Wasach Range of UT, but not between the San Juan Mountains and the Front Range of CO.

The techniques used to create seed transfer guidelines for trees have been refined based on the work of Rehfeldt (for example Rehfeldt 1988, 1990a,b, 1991, 1993, 1995, 1999). For ponderosa pine (*P. ponderosa* var. *scopulorum*) in southwest Colorado (Figure 6.1), seed transfer zones based on studies with juvenile trees (Rehfeldt 1993) are very different from seed zones drawn by Cunningham (1976). The zones allow greater distance in east-west than north-south transfers, and restricted movement between elevation bands. Elevation, latitude, and a gradient in summer precipitation has much higher explanatory power than longitude. In contrast, seed transfer of pondersa pine in Montana emphasizes north-south transfers (Figure 6.2). Even though timing of shoot elongation and winter desiccation was an important adaptive trait in these studies and strongly influenced by elevation, these maps do not correspond to plant hardiness zones (Figure 6.3). The hardiness zones do not correspond well to ecoregion maps either (Figure 6.4).

Recently, forest geneticists have furthered this work by developing “Expert Knowledge Base Systems,” which are computer programs to guide decisions for deployment of seeds of tree species that have been studied in detail, including ponderosa pine in Region 2 (Mahalovich 2003). Parker (1992, 1996) developed the concept of focal points seed zones where one uses common garden data and geographic information systems (GIS) to produce maps that show suitable seed sources for a given planting site (that is, the focal point). Such methods can serve as a model for seed transfer research for many non-tree species. However, additional types of studies may be warranted depending on the life history, gene flow potential, and breeding system of the species.

Common garden studies with hybrid progeny tests evaluate risk of outbreeding depression. In their quest to understand the nature of species differences, the Carniegie group did an enormous amount of hybridization and cytological work on annual and perennial plant species. The studies often included multiple populations of the same species and related species (Clausen et al. 1940, 1941; Hiesey et al. 1971; Hiesey and Nobs 1982). Some of their work identified evidence for heterosis while other work showed reproductive isolation through crossing failure, hybrid inviability, hybrid infertility, or decreased hybrid vigor. Detailed cytological studies were done in association with the hybrid performance work to examine the importance of chromosome structure and ploidy on outcomes.

Crosses were sometimes carried to the F2 or F3 progeny (second and third generation offspring) (for example species of *Madia*, *Layia*, *Zauschneria*, and *Mimulus*), but the early studies were not clearly presented in terms of mean population fitness. The actual risk of population declines or benefit of population increase from hybridization usually was presented qualitatively in terms of general failure of hybrids, infertility, or a general increase in vigor. In contrast, data on F1 hybrids between species and parental lines, such as those in the *Poa pratensis* and *P. ampla* complex planted in common gardens across the country, were presented in more detail (Hiesey and Nobs 1982). Though not statistically analyzed, graphs of the *Poa* data revealed qualitative differences in the mean fitness of parental and hybrid lines in different habitats, including some evidence for environmental dependence of outbreeding depression.

The grand scale of the Carniegie group's experiments set the stage for future studies and improved statistical analysis. Recent work by Fenster and Galloway (2000) in North America on the partridge pea (see Chapter 5, Chapter 10), and work in Europe by Keller et al. (2000) on three native colonizing species, quantified fitness outcomes from hybridization of divergent populations. Such studies, together with work by Edmands (1999) on a marine copepod, set a new standard for analyzing risk of outbreeding depression in addition to discovering maladaptation. The plant studies included parental generation, F1 (first generation of offspring) and F2 hybrids of multiple populations (plus the F3 in partridge pea) in multiple common gardens across a large part of the species' ranges. All these studies used traditional line-cross analyses from the field of quantitative genetics (Lynch and Walsh 1998). The analyses allow determination of the genetic basis of fitness traits and if there is outbreeding depression in the F1 or subsequent generations, hybrid vigor, or some combination. Results of the partridge pea and other studies are discussed in Chapter 5. Briefly, some F1 crosses between different pairs of partridge pea populations showed heterosis. Of these, the most geographically distant pair of populations suffered reduced fitness in the F3 generation, below that of the mean of the parental populations. There was hybrid breakdown and outbreeding depression.

Integrating genetic marker data, progeny tests, and common gardens. Additional methods are needed to quantify the risk of outbreeding depression relative to environmental variables or to genetic distance. This was accomplished in part, by the work of Edmands (1999) on a marine copepod, and by Montalvo and Ellstand (2001b) on the subshrub *Lotus scoparius*. These studies integrated common garden studies with information from molecular markers to identify if the risk of outbreeding depression increases with genetic distance or features of the environment.

A number of ecological genetic models predict increasing declines in fitness as genetic differentiation of the crossed populations increases (Orr and Turelli 2001, Turelli et al. 2001, Edmands 2002, Edmands and Timmerman 2003). This relationship has been demonstrated empirically in several studies that examined populations over a geographic region or large geographic area (for example, Hughes and Vickery 1974, Vekemans and Lefebvre 1997, Edmands 1999, Montalvo and Ellstrand 2001). This increasing relationship is not expected to occur until after outcrossing distances have exceeded the point at which outbreeding recovers fitness losses due to inbreeding depression (Waser 1993, Kaye 2002). In addition, under certain genetic architectures, the relationship cannot be observed until after the F1 generation.

Crosses between genetically differentiated populations can result in an immediate or delayed reduction in fitness (outbreeding depression), no change in fitness, or an increase in fitness (hybrid vigor or heterosis) (Figure 6.5, see also Chapter 5). The outcome depends on the underlying genetic architecture of traits, including dominance and epistatic interactions, and if there are differences in local adaptation. When local adaptive differences exist, the dilution of adaptation that occurs in the F1 can recover a bit in the next generation because some of the original adapted genotypes will be reconstituted when F1s mate with each other or backcross to parents (Figure

6.5.A). However, when there is intrinsic coadaptation, some genetic architectures cause no change in fitness or heterosis in the F1, followed by outbreeding depression in the F2 or subsequent generations (Figure 6.5.B and D, respectively). This occurs when beneficial combinations of genes (not necessarily influenced by the environment) are broken up during cell division and recombination (Lynch 1991, Hufford and Mazer 2003). The original beneficial genotypes can also be recovered to some extent in subsequent generations, but the lack of fitness can persist for a long time. Finally, there is one situation in which heterosis decreases in the F2 or F3, but not below the mean fitness of the parents (Figure 6.5.C). In this model, the heterosis persists. In the absence of F1 outbreeding depression, if one wishes to know what will happen to mean fitness with increasing differences in the genetic distance of parental source populations, the analysis needs to be done in the F2, F3 or backcross generation (for example, Edmands 1999).

Hufford and Mazer (2003) reviewed the reasons for different fates of hybridization after translocation and recommend that hybridization effects be included in the determination of seed transfer guidelines. In addition, they coined the term “epitype” to describe populations that are genetically differentiated because they have adapted to *specific genetic backgrounds* (intrinsic arrangement of interacting genes, coadapted gene complexes). This differs from traditional “ecotypes” that have adapted to particular external environments (extrinsic adaptation).

If multiple populations are crossed with each other and the parental source populations are grown together with progeny in a common garden, the risk of outbreeding depression can be assessed. For F1 progeny, a regression of fitness on genetic distance of crossed populations can identify the risk of outbreeding depression due to differences in intrinsic coadaptation. A positive slope indicates increased fitness on average (hybrid vigor), and a negative slope indicates decreased fitness (outbreeding depression). If there is hybrid vigor, the testing should also occur with F2 and possibly F3 progeny to check for hybrid breakdown. In contrast, environmental dependence of fitness is identified in the F1 generation by a significant decrease in performance as the difference in the test environment relative to the environment of the two parental source environments increases (Montalvo and Ellstrand 2001). In other words, if there is a break up or dilution of adaptation, fitness will decrease as the environmental difference increases. In both types of test, the sign and slope of the regression quantifies the risk. If the slope is significantly negative, the steeper the slope, the higher the risk. Presumably, as recommended by Rehfledt for provenance tests, a least significant difference can be calculated to guide how far seed movement along an environmental or genetic distance gradient results in a significant decrease in fitness.

Use of molecular markers in seed zone research

Compared to analysis of quantitative traits in common gardens, molecular marker studies are faster, less labor intensive, and can be less expensive. They can help researchers refine population choices for common garden tests and fine tune seed transfer guidelines based on quantitative genetic data. They have the added benefit of uncovering landscape level patterns in presumably neutral genetic variation. Westfall and Conkle (1992) describe how markers can be used to reveal geographic patterning of populations. Geographic patterns in neutral markers can be useful for determining evolutionary histories of populations, defining subspecific taxa, and the likelihood that there will be mating incompatibilities, factors important to seed transfer guidelines.

Populations that have become isolated can become adapted to different environments. Although molecular marker patterns rarely reveal adaptive patterns, they may reveal the possibility that populations have taken different paths toward adapting to similar, but spatially distant environments. If distant sites are environmentally similar, common garden studies can reveal if the populations are similarly adapted to the physical environment. If the populations have become adapted by different mechanisms, a common garden study would miss that fact. Molecular markers, however, would be able to detect significant genetic differences among the populations. Seed transfer guidelines based only on adaptation might allow deployment of seeds to distant areas even though the populations have accumulated many differences over time, including different adaptive solutions to similar environmental problems. The accumulated differences could lead to differences in intrinsic coadaptation that would be exposed *after* hybridization of populations (Chapter 5), even though populations are redundant in adaptation to particular conditions.

Molecular marker variation can also provide an understanding of the historical relationships of populations that cannot be obtained from analysis of quantitative traits. As pointed out in Chapter 5, molecular markers can reveal the more ancient patterns of population dispersal overlaid by newer patterns revealed from analyses of quantitative traits. Molecular markers also provide data for assessing genetic distance and relatedness of populations. As explained in the previous section, genetic distance can sometimes be used to predict the magnitude of outbreeding depression due to differences in intrinsic coadaptation. Furthermore, when used in concert with common garden studies, the slope of the regression of fitness on genetic distance represents the magnitude of risk.

Phylogeographic studies can reveal spatial patterns in gene migration and genetic similarity of populations useful to the fine-tuning of seed transfer guidelines. They can identify potential areas of hybridization between divergent populations that have regained contact and the degree of natural introgression. The geographic pattern in molecular markers can also be used to identify gaps in gene flow and genetic similarities that could correlate with the existence of different “epitypes”. These gaps represent areas of higher risk of outbreeding depression due to differences in coadaptation. More highly differentiated populations are also expected to have a higher potential of being different ecotypes, and therefore a higher risk of being adapted to different conditions. Molecular studies can help to maximize choice of populations to be used in lengthy common garden studies so that risk can be more accurately quantified. A great deal of information from genetic marker variation and studies of quantitative traits are complementary.

Comparing divergence in quantitative versus molecular traits to estimate risk

The labor and time required to run experiments that quantify risk of outbreeding depression and maladaptation at spatial scales relevant to restoration discourages their use. It has been proposed that the evolutionary mechanisms responsible for genetic patterns over the range of a species can have a large influence these translocation risks. This is because gene flow drives the formation of patterns in neutral traits, while selection drives the formation of pattern in adaptive traits. Consequently, simultaneous assessment of population structure determined from adaptive traits (Q_{ST}) and structure determined from neutral traits (F_{ST}) could help in estimating what mechanisms underlie current patterns of population differentiation. For any particular geographic area (for example, the extent of a species’ distribution in Region 2), the higher the values of Q_{ST} and F_{ST}, the more pronounced the population differentiation over the sample region, and the higher the translocation risk. In addition, the magnitude and relative size of these measures may indicate the relative risk of outbreeding depression caused by differences in local adaptation relative to risk due to intrinsic coadaptation.

Comparisons between Qst and Fst will be much more meaningful if the quantitative traits used in the analysis have obvious links to fitness. For example, quantitative traits such as timing of leaf flush and flowering can have profound consequences on survival and reproductive success. Floral traits can have a large influence on pollinator visitation, pollen dispersal, and seed set. Yang et al. (1996) proposed the following model for evaluating the relative size of Q_{ST} and F_{ST}, where Q_{ST} is assumed to be based on traits with adaptive variation.

> If $Q_{ST} > F_{ST}$, then divergent selection may be invoked. This suggests that selection is directional and stronger than gene flow causing populations to become adapted to different environments (local adaptation).
>
> If $Q_{ST} = F_{ST}$, then cannot reject null hypothesis of random genetic drift. This may indicate gene flow counters formation of local adaptation in the measured traits.
>
> If $Q_{ST} < F_{ST}$, convergent selection may be invoked as a cause for reduced genetic differentiation. There may be strong stabilizing selection and an opportunity for evolution of coadaptation.

The magnitude of these statistics also has connotations. If Q_{ST} is large and much greater than F_{ST}, then the potential for ecotypic differentiation is high and the associated risk of translocation is high. If F_{ST} is large, there is a higher probability that different epitypes have evolved, but it does not reveal the form of the gene interactions. In a review of species that had values of both F_{ST} and Q_{ST}, McKay and Latta (2002) found patterns that suggest Q_{ST} is a better predictor for preservation of adaptation to local environments while F_{ST} is a better predictor of the pattern of allelic differentiation. In another review, Howe et al. (2003) found that north temperate tree populations are often well differentiated for traits related to adaptation to cold and usually weakly differentiated for molecular genetic markers. That is, Q_{ST} in adaptive traits generally exceeded F_{ST} (for example in Douglas-fir, lodgepole pine, sitka spruce, western larch, white fir, quaking aspen).

This method may be more useful if it is used in tandem with assessing the measured quantitative variation for evidence of clinal versus ecotypic variation. The panel is not in yet about this model's predictive power. The model will depend on the geographic scale of sampling. As with common gardens, if samples contain large gaps in actual population variation, clinal patterns may not be detected and ecotypic variation may be overemphasized.

Species interactions and translocation risk

The effects of translocation risk in relation to adaptation to the biotic environment, including interactions with other plants, pollinators, pathogens, herbivores, remains understudied. There is often geographic structure to plant-animal interactions and plant-pathogen interactions and susceptibility that may reflect adaptive differentiation (Thompson 1999, Thompson and Cunningham 2002). The potential effects of species interactions on translocation risk can be assessed if provenance tests are carried out in contrasting native environments. For example, Rehfeldt (1995) included the effects of a *Meria* needle cast and survival (not necessarily related to the needle cast) in provenance tests and analysis of seed transfer risk for *Larix occidentalis*. However, some potentially important interactions, such as effects of interspecific competition or effects of native fungi can be missed unless experiments are set up in native soil in native habitat.

Sometimes risk of disruption of plant-animal interactions can be inferred but difficult to assess quantify within a regular provenance test. For example, in a recent study, Siepielski and Benkman

(2004) found evidence that variation cone size and cone scale thickness in lodgepole pine *(Pinus contorta* var. *latifolia*) was associated with conflicting selective pressures by three species of seed predators that co-occurred with the tree in different parts of its geographic range. Presence of red crossbills results in larger cones with thicker scales, absence of pine squirrels results in cones with more seeds and a higher ratio of seed mass to cone mass, while presence of borer moths selects for smaller cones with fewer seeds. Changes in cones through selection imposed by crossbills results in higher susceptibility of seeds to borer moths. In contrast, selection on cones by squirrels reduces predation by the moth. Although not mentioned in this study, there may also be an adaptive pattern of cone scale thickness and serotiny in lodgepole pine that correlates with fire frequency. In addition, cone size can be determined by the success of pollination (M. F. Mahalovich, pers. com.). Because the form of the environment-by-genotype interaction may vary over years as populations of interacting organisms change, adaptive patterns in plant traits associated with species interactions may be harder to detect than patterns in physical environment.

Ecological genetic models and understanding risk of extinction

As was pointed out in Chapter 5 and in Figure 6.5.C, some hybridization can be a good thing and much speciation has been influenced by hybridization of populations. However, the uncertainty of the outcome of hybridization from human movement of populations, if it will be good or bad for fitness, calls for an assessment of risk. There have been recent efforts to model the risk of extinction and changes in mean fitness of populations following translocation and hybridization. In a review of both animal and plant data, Edmands (2002) found that although the hybridization success often decreases with increased genetic differentiation of crossed populations, genetic distance by itself was not a strong enough predictor to guide management decisions. For this reason, Edmands and Timmerman (2003) used models to examine the usefulness of additional genetic factors in predicting effects of population hybridization. After hybridization, the pattern of mean population fitness over time and the number of generations that fitness was lowered together influenced the risk of extinction. Outbreeding depression increased with increased genetic distance, but the initial fitness drop and number of generations it took to recover higher fitness depended on the genetic and ecological reasons for the initial loss in fitness. For example, differences in local adaptation (as in different ecotypes or opposite ends of a cline) caused higher initial outbreeding depression, whereas differences in intrinsic coadaptation (as in different epitypes) caused recovery of original fitness to take many generations. The pattern and duration of fitness loss depended on a number of factors in addition to the genetic basis of outbreeding depression, including mating system, relative population size, how often mutations occur, and the genetic similarity of the hybridizing populations. When genetic distance was held constant, the magnitude of outbreeding depression, and thus extinction risk, increased with amount of outcrossing, and several other factors. Their model was generalized to fit plants or animals.

Wolf et al. (2001) used an ecological model to estimate risk of extinction following hybridization of plant species. The model did not include different genetic systems. It did not include genetic configurations that lead to intrinsic coadaptation, but it did allow fitness to vary depending on differences in adaptation to the environment. They incorporated many factors in their model, including variation in population size, mating system, amount of pollen produced, success of pollen tubes in fertilization, competition between seedlings, and habitat dependence to estimate the fate of hybridizing populations and their hybrids. They estimated if both parental populations and the hybrid population would persist, if one would displace the other two populations, or if there would be complete mixing of the gene pools through introgression (see Chapter

5). Differences in local adaptation between parental populations and hybrids made a big difference in extinction risk. Multiple habitats were required for persistence of all populations. The authors applied the model to actual data from three studies of hybridizing species to estimate extinction probabilities for those cases. Although the authors concentrated on hybridization among species, the models can be applied to hybridizing populations of the same species. Other extinction risk models have concentrated on factors such as population size, fragmentation of populations, availability of mutualists, orientation of populations, dispersal ability, and mating system (Lynch et al. 1995, McCauley et al. 2001, Lennartsson 2002).

Together, these studies show how different plant attributes, in addition to differences in adaptation and genetic systems can influence the risk of translocation and aid in refining seed transfer guidelines. Any time the average fitness of a population declines after hybridization, as shown by these models and by actual experiments, this represents an increase in extinction risk. Models still need to be developed that predict if there will be important interactions among alleles or among loci when genes that have not heretofore been placed together, combine in a hybrid individual. No one knows the probability that a particular pair of populations will have a genetic architecture upon hybridization that is conducive to outbreeding depression versus heterosis. However, some useful generalizations have come from the modeling efforts presented above. As pointed out in Chapter 5, information on life-history traits, population size, and population diversity statistics can aid predictions about how *differentiated* populations might be and if they are more or less prone to inbreeding depression.

Summary

Considering risk of translocation is not new, but current interpretation of risk, means of evaluating it, and risk avoidance procedures have been refined over the years. There is a long history in forestry, agriculture, and more recently in fisheries of considering how adaptive differences among populations affect success of translocated populations. It is well recognized that maladaptation is something to be avoided. Current methods for developing continuous seed transfer guidelines in forestry are capable of determining if populations are genetically local with regard to risk of extinction from maladaptation. Fortunately, this simple concept is consistent with management of biodiversity and is easily transferred to use of native plant materials for revegetation.

The same cannot be said with regard to considering adverse effects from hybridization. Techniques for identifying and quantifying risk of extinction from hybridization have not been applied widely. This may not be necessary for most temperate commercial tree species. Most tree species for which continuous seed transfer guidelines have been developed have high rates of gene dispersal and little population structure on a regional basis. When assessed together with often higher geographic patterning of quantitative traits relative to molecular markers ($F_{ST} << Qst$), this suggests that the risk of outbreeding depression is lower than the risk of maladaptation. In contrast, the non-tree species used in restoration show a diversity of life-history and gene dispersal capabilities, often have more structure to their populations (in molecular markers), and may be more prone to experiencing outbreeding depression (for example if $F_{ST} \geq Q_{ST}$).

As explained in Chapter 5, many plant species have been influenced positively, and many have formed, by past hybridization events. However, evidence of introgression and hybrid speciation does not reveal the relative number of past hybridization events resulting in failures or population extinctions. Past hybridization events, before human intervention, occurred as plants slowly migrated and came into contact. Humans drastically increase the rate of migration, skipping propagules over large expanses and geographic barriers. To keep seed transfer within genetically local areas, guidelines should consider the balance between the beneficial effects of decreased inbreeding depression and hybrid vigor, relative to the detrimental effects of outbreeding depression, including hybrid breakdown. This balance will rely on the magnitude of genetic divergence, species attributes, and the underlying genetic architecture of traits influencing fitness. The mechanisms that cause incompatibilities among mated populations influence the continued divergence, merging, or extinction of populations over a range of environments. Seed transfer guidelines for many restoration species would benefit from studies that examine the results of hybridization for multiple generations.

Given such research is generally lacking, we provide tools (Chapter 8-10) for weighing *existing* knowledge about particular species so that reasonably informed decisions about seed sources and types of plant materials can be made. Until there are results available for a diversity of species, it will be necessary to rely on the patterns revealed by theoretical models and simulations.

Figure 6.1. Comparison of historic and revised southwestern ponderosa pine seed transfer rules for Colorado in Region 2. Grey areas = distribution of ponderosa pine; red lines = historic seed zones (Cunningham 1976); blue lines = revised transfer zones based on Rehfeldt (1993). Map is based on a sketch provided by M. F. Mahalovich. Note: these lines are approximate.

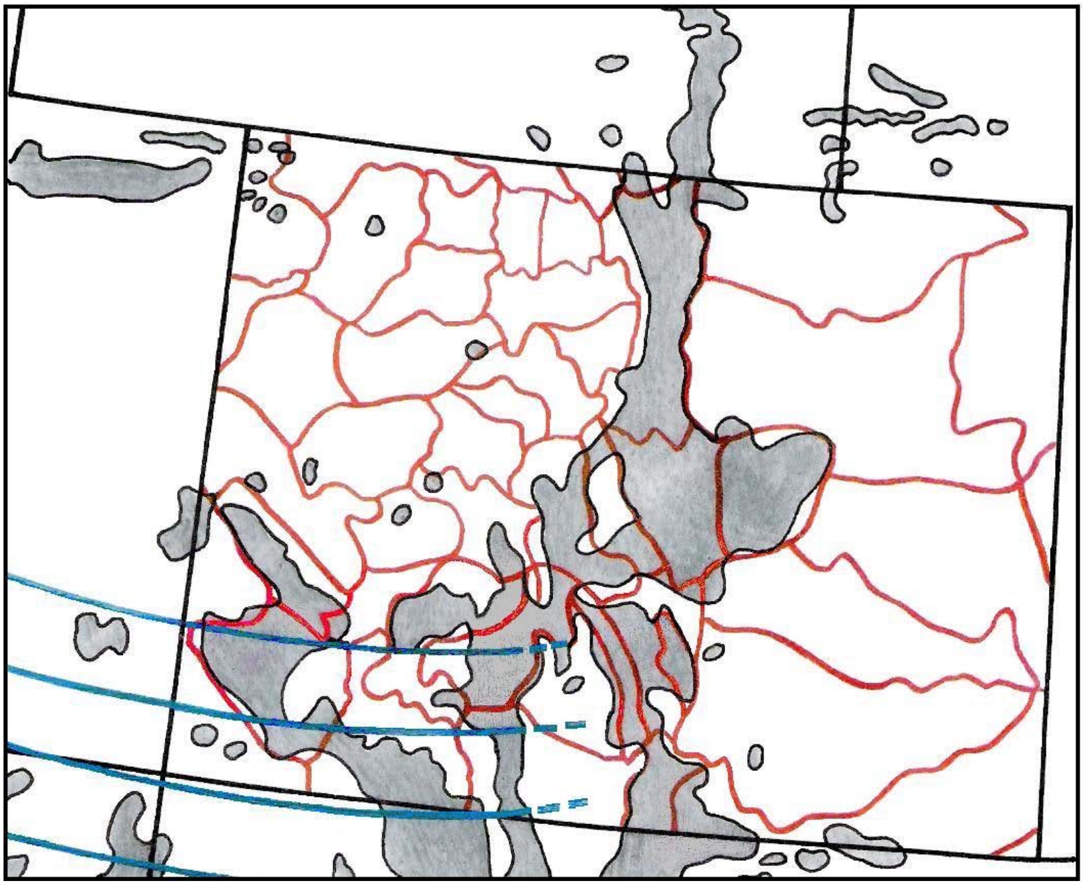


Figure 6.2. Example of species-specific seed zones for Ponderosa pine (var. *scopulorum*) in Regions 1 and 2. This map shows seed zones for Montana and northern Wyoming. Within each of the six zones, the maximum movement allowed among elevations is 700 ft if collected below 4000 ft, and 1000 ft if collected above 4000 ft. After map provided by M. F. Mahalovich.

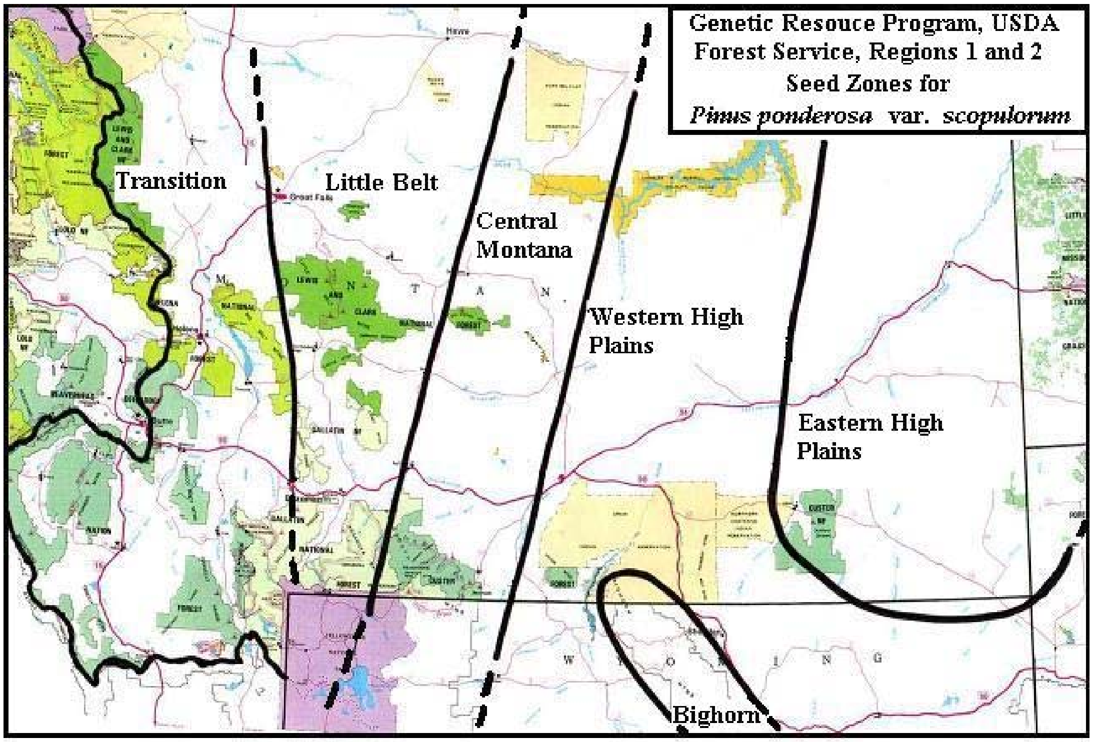


Figure 6.3. USDA plant hardiness zones for central US showing range in average annual minimum temperature. States area outlined in black. Hardiness zones are sometimes used in conjunction with elevation, habitat, Major Land Resource Areas, ecoregion maps, and ecological genetics information for particular plant species in designing seed transfer guidelines. Modified from US National Arboretum web site version of map in USDA Miscellaneous Publication No. 1475.

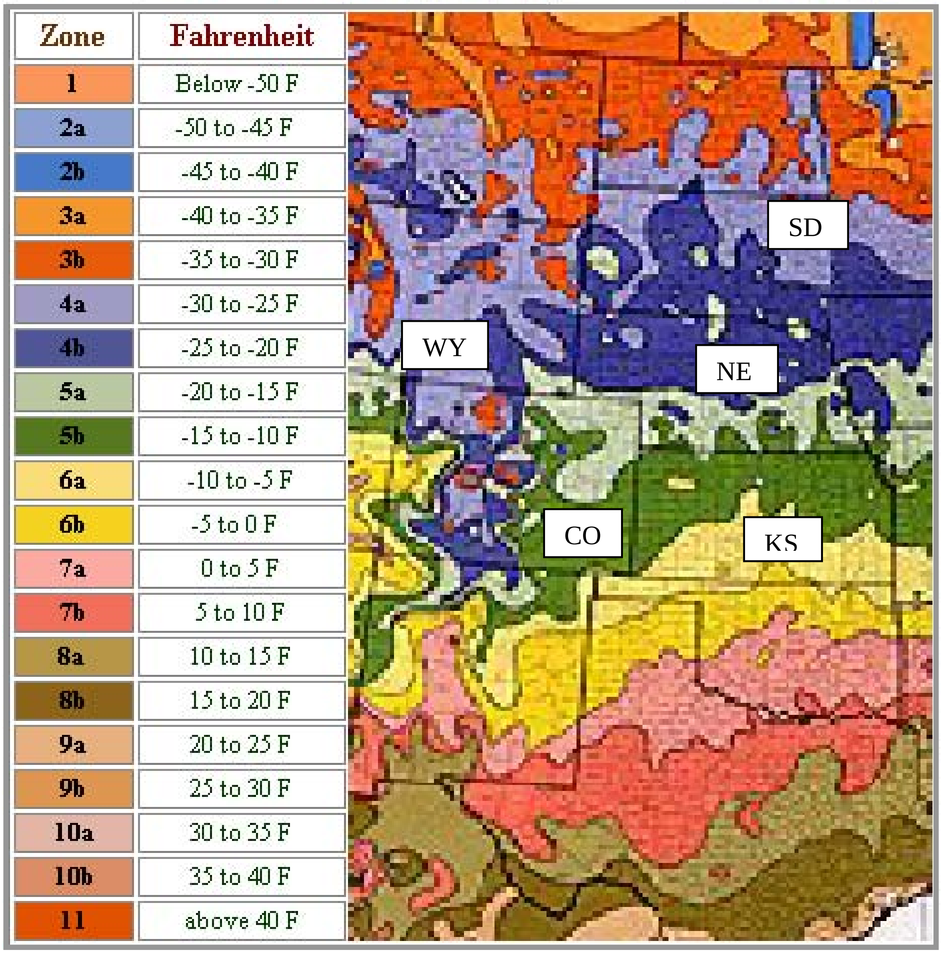
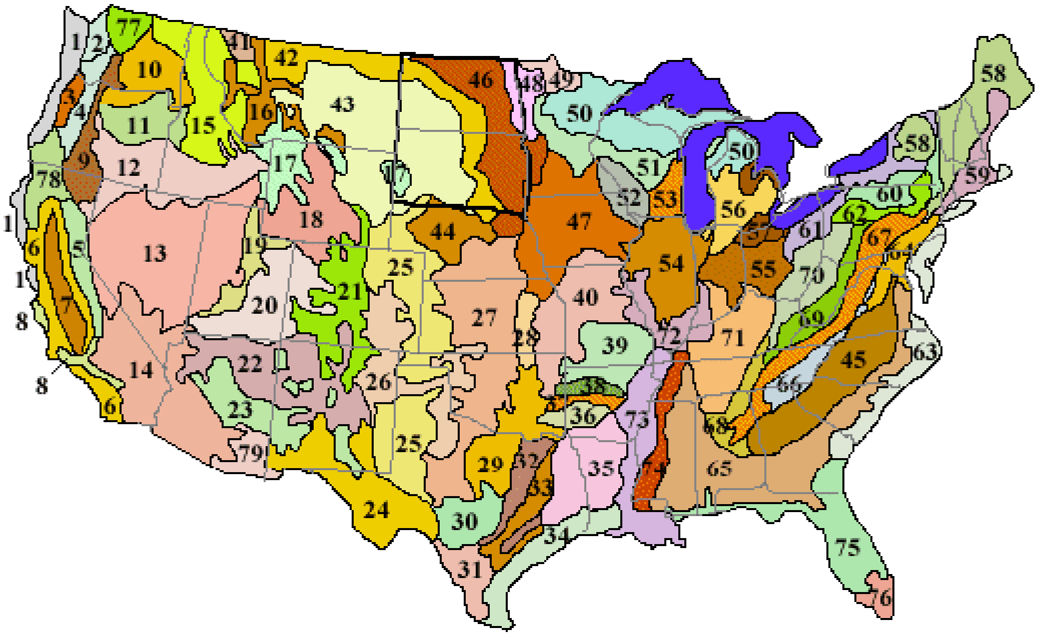


Figure 6.4. Ecoregion maps for United States and South Dakota (Bryce et al. 1998). Level III Ecoregions (A) are broken up into finer, lettered divisions in the Level IV Ecoregion maps (B) based on ecological and climatological factors. The ecoregions of South Dakota (B) tend to run north-south and are very similar to seed zones of Cunningham (1976, see Figure 9.2).

A. Level III Ecoregions of the Conterminous United States



B. South Dakota Ecoregions, Level IV

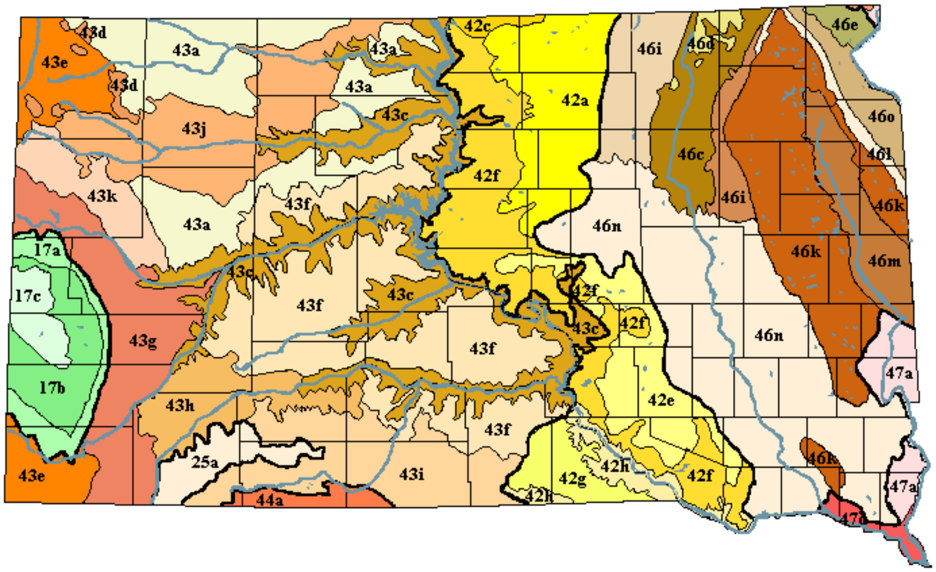
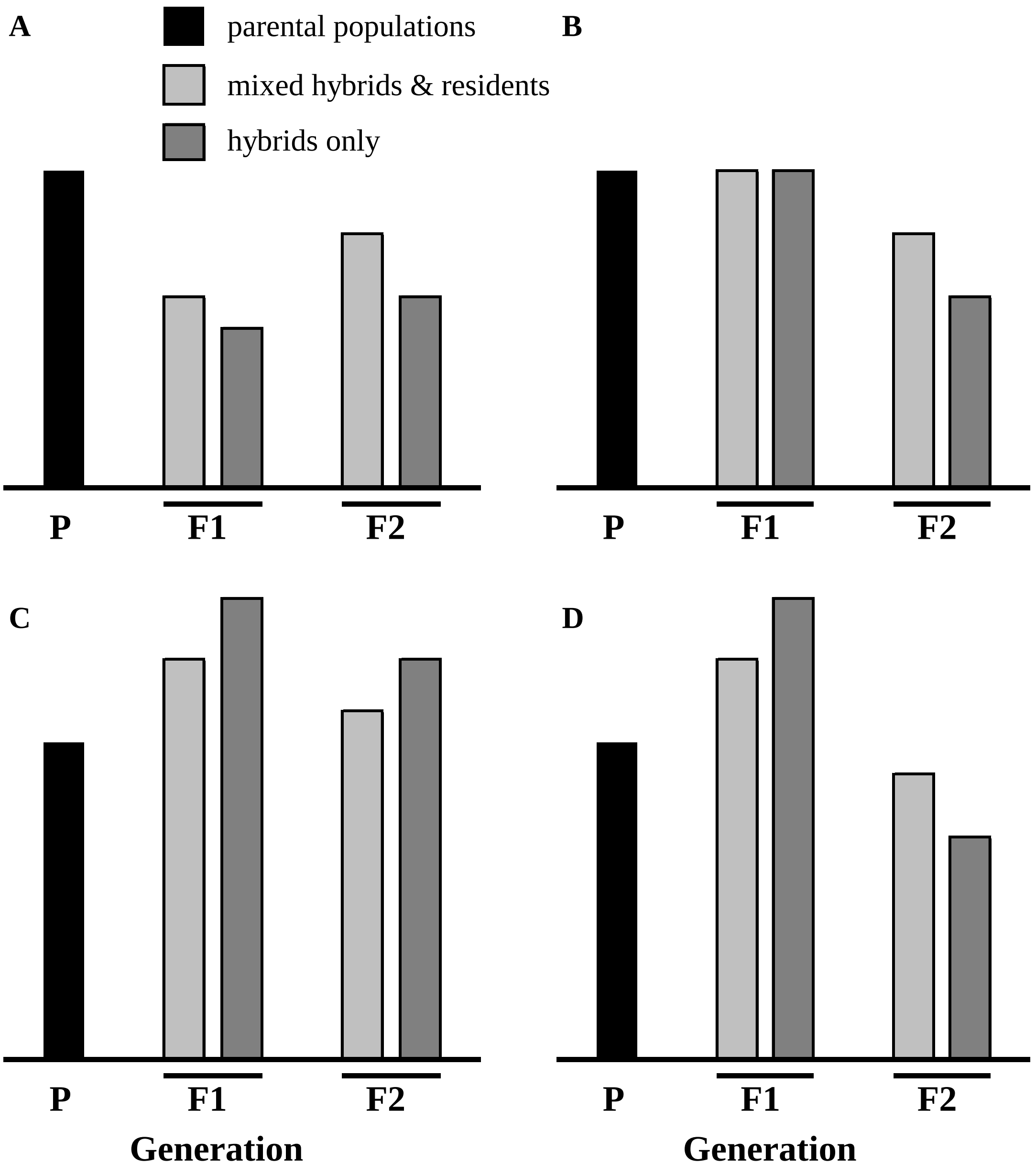


Figure 6.5. Four of the possible fitness outcomes of population hybridization following mixing of a resident and genetically non-local population. The height of the bars is the mean fitness of populations at each generation: P = parental generation; F1 = first generation following hybridization; and F2 = second generation following hybridization. When mixtures of populations mate successfully, both hybrid and resident genotypes will be present in the F1 and F2 generations. Black bars represent the mean fitness of the two parental populations (resident plus translocated population); light gray is the mixture of parental genotypes and hybrids, and dark gray is just the hybrids. Based on Hufford and Mazer (2003).



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Chapter 7

Fitness Consequences of Poor Genetic Matching

The expression “poor genetic matching” is used here as a short-form reference to a situation where genetically inappropriate plant materials are introduced to a project site. In Chapter 1, 13 reasons were provided for carefully selecting appropriate genetic sources for planting projects involving native plant species. In theory, the consequences of failing to consider the genetic source of plant materials in these situations or of making an inappropriate choice can be directly inferred from those 13 statements. Consequences of poor genetic matching (between the introduced plants and the site conditions) could include outright mortality, loss of ability of the plant population to remain viable in the long-term and to adapt to changing environmental conditions, loss of genetic (and hence, biological) diversity, negative impacts in the broader ecological community arising from restoration failure, lost investments, and so on. One serious related issue is the wastage of the mismatched genetic materials, which could be valuable and limited in supply (see Box 8). The potential consequences onsite span a broad range—from negligible to dramatic. In general, in the presence of local adaptation or incompatible genomes, inappropriate choices in matching the genetic source of plant populations to the revegetation site can, in the extreme, undermine the survival ability of the introduced plants and plants resident to the planting area. Alternatively, the mismatch may not be as severe and manifest as lowered viability and survival over several generations resulting in stress. In tree species at least, this situation leads to stress-cone crops and contamination of local gene pools via wind pollination and seed dissemination.

This chapter focuses on unintended consequences. The management objective assumed is one of maintaining or restoring natural levels of genetic diversity and spatial genetic structure of genetic diversity and increasing the potential for long-term viability. However, if the management objective differs from this, or the introduced plants or seeds are only intended to serve a short-term purpose, such as improving the soil or stabilizing the soil surface, then poorly matched genetic sources of native plants, or exotic plant species, may be appropriate. For example, nurse crops of a different species are sometimes used to help establish native forest tree species. However, if there is a potential to adversely affect nearby populations, the choice deserves further scrutiny and consideration of alternative plant materials. It is important to ensure that the exotics or mismatched natives do not have the potential to become invasive, and that the natives—if poorly matched genetically—are so poorly matched that they will not flower, produce seed, or vegetatively spread in their new environment. This can be a tricky management scenario, as even very poorly matched native plants might occasionally flower and set seed with an unusual weather event, possibly distributing pollen to nearby native plant populations.

That the consequences of genetic mismatching can be serious and are recognized at higher management and public levels is illustrated by a similar situation and concern over gene flow from transgenic (or genetically modified) crops (see, for example, Ellstrand 2003). Although this general topic represents a spectrum of subjects (such as gene flow from crops to related native species, environmental impacts, intellectual property rights, and control over crop germplasm), the underlying genetic issue is the unintended flow of genes from crops (in this case, genetically modified through nontraditional methods) to other plant species, either native or non-native. Unintended consequences could be the introduction of genes for herbicide resistance into weed or native plant species from a transgenic crop that had been engineered for that trait. Concern over this possibility has been expressed by the Forest Service, for example, in response to the APHIS proposal to deregulate a genetically modified form of creeping bentgrass or turfgrass (*Agrostis stolonifera* L.) that is resistant to glyphosate—the active ingredient in the herbicide *Roundup* ® (Gladen 2004). Gene flow from genetically modified bentgrass into other plants of the same species has been documented for distances up to 21 km, although impacts on progeny or the structure of resident plant communities has not yet been investigated (Watrud et al. 2004). Although there has not yet been widespread use in the US of genetically modified forest tree species, discussion of how this might impact the environment is warranted. At least 33 species of transformed forest tree species have been successfully regenerated. Target traits in these species are often herbicide tolerance, insect resistance, disease resistance, abiotic stress tolerance, wood quality and quantity, and reproductive development (van Frankenhuyzen and Beardmore 2004). The likelihood of genes flowing from the genetically modified crops into native plant species is not necessarily any different than the likelihood of genes flowing from genetically mismatched plants that have been planted as part of a restoration effort. Much will depend on the context—opportunity for pollination, any natural selection on the hybrids that may arise, and so on. Although the spectre of transgenes moving into weedy or native plant species is much more dramatic (because most inserted genes are highly unlikely to ever show up as a natural mutation), it is the same principle discussed here in the context of providing appropriate genetic matches when restoring or replanting the native plant species. The consequences of gene flow from mismatched plants into the resident native populations are largely unknown, but potentially serious.

The spectrum of consequences

Although the potential consequences are varied, they can be categorized for simplicity: those to the introduced plants themselves (or their progeny) and those to the neighboring plants or those in sufficiently close proximity to be affected. The consequences for the introduced plants can be immediate and dramatic (such as when the seeds don't germinate or the plants die quickly, before reproducing, because of severe maladaptation). For example, in a rangewide provenance test of ponderosa pine (*Pinus ponderosa* P. & C. Lawson) planted in Colorado, seedlings from California and Oregon locations were killed by frost in the first year, while seedlings from local sources survived (Squillace and Silen 1962). Alternatively, and probably more typically, lack of or lowered local adaptation may be expressed gradually, in terms of somewhat lower survival rates or lower reproduction per generation. And, if the plants do survive to reproductive maturity, their modest maladaptations may be experienced as environmental stress—a condition that typically can cause a shift towards reproductive output. That is, stressed plants often allocate more resources to reproduction rather than vegetative growth. Likewise, the environmental variation to which there is some local adaptation by the native populations (and maladaptation by the introduced plants) may only occur infrequently or over long periods of time. The introduced plants and their progeny may survive and reproduce under typical climatic conditions, but fail with the rare frosts or droughts that play an important role in molding the resident population (Chapter 6). These impacts assume a context where local adaptation of the native plant species occurs: this is not always the case.

The consequences may extend beyond the planted population if the introduced plants survive to reproduce and then spread their genes to neighboring individuals or sites. Genes are difficult to herd or reign in after they are unleashed. This gene flow is undesirable if it results in outbreeding depression—a decline in fitness in subsequent hybrid (between the introduced and resident plant populations) generations (see Chapter 5). This effect is related to the breeding system and reproductive biology of the plant species. Genetic impacts through hybridization with neighboring resident populations will occur if the introduced population is capable of cross-pollinating with resident plants. If flowering times of the two populations do not overlap, the species is strictly self-pollinating, or both populations only reproduce vegetatively, then this problem will not exist. However, even in self-compatible species such as the perennial herb *Aquilegia caerulea* James, there is still some degree of outcrossing and the relative amounts of outcrossing and selfing varies among individual plants (Brunet and Eckert 1998). Consequently, the risk of genetic contamination may be lower for self compatible plants, but rarely, if ever, zero. The terms genetic contamination or genetic pollution are often used to describe this undesirable gene flow from the non-local introduced plants to the native resident plant populations (see Rhymer and Simberloff 1996, Potts et al. 2003). Many plant species are neither strictly outcrossing nor self-pollinating, and the consequences vary accordingly. In general, when the probability of outcrossing with resident populations is low, then the risk of genetic pollution is also low. However, it is important to remember that when hybrids *are* produced that involve translocated populations with low outcrossing rates, there is a greater likelihood that they will be less fit than the parental populations. This is in part because such populations have restricted pollen dispersal and a higher probability of the newly mixed populations being genetically differentiated.

Outbreeding depression can be the result of causes other than simple maladaptation of the introduced genes (Chapter 5). Hybridizations between two differing populations or subspecies can break up compatible, beneficial combinations of genes (called coadapted gene complexes) (reviewed by Hufford and Mazer 2003). Furthermore, differences in ploidy levels are not infrequent among populations of the same species. Mixing different ploidy levels often results in mating incompatibilities (reviewed in Levins 1978).

In addition to the consequences of genetic mismatching for the introduced plants and their progeny and for the neighboring resident plants of the same species, there could be cascading effects throughout the ecological community (as suggested in Chapter 1). Direct consequences are easily envisioned for pollinators and seed dispersers. Introducing plant populations with earlier or later (than the resident plant populations) flowering and seed production times, for example, could have dramatic consequences for associated animal species.

The overwhelming majority of genetic mismatches would be predicted to have negative consequences. However, in a few cases, there might be a beneficial effect. For example, if a resident plant population has been reduced in size and has lost considerable amounts of genetic diversity, then the infusion of more genetic diversity from (certain) other populations might assist the resident population and improve its potential to adapt and persist in the long-term. This process occurs in nature under certain conditions, such as when small populations of a native plant species that are experiencing some level of inbreeding depression are alleviated with new genes that occasionally arrive through pollen from other populations. This occasional influx of genetic diversity, because it could theoretically prevent extinction of such small populations, has been called the "rescue effect" (Brown and Kodric-Brown 1977). For example, experimental cross-pollinations between small populations of scarlet gilia (*Ipomopsis aggregata* (Pursh) V. Grant) and a large, distant population improved seed mass and percentage of germination in the small populations. The small populations were experiencing some loss of fitness related to their small size, which contributed to inbreeding depression, genetic drift, or both (Heschel and Paige 1995).

The term "genetic rescue" is now more commonly used to describe the situation where a resident population's probability of survival is increased (over that which would normally occur) through immigration of genes from another population (Richards 2000). More recently the term has been used in conservation biology as a potential tool for supporting endangered plant populations. Determining when genetic rescue is likely to occur, rather than a neutral or negative consequence, is a complicated pursuit as it is based on genetic, environmental, and demographic factors and their complex interactions (Tallmon et al. 2004).

A second example of potentially beneficial effects of genetic mismatching is that of hybridizations between different populations or subspecies in the presence of new or highly variable environments. Although in most cases of plant hybridizations under field conditions the hybrids are less fit than their parents, if there are new or variable environmental conditions, then it is possible that the hybrids would be more fit under those conditions (Arnold and Hodges 1995, Campbell 2004). But because such situations are relatively rare, and because genetic mismatching more often has deleterious rather than beneficial consequences, the focus in this chapter remains on the former.

Real-life examples of consequences of genetic mismatching are rare

Proven examples of planting projects that have failed primarily or entirely for genetic reasons are difficult to find. Given that there are many published studies of controlled planting trials that document adverse consequences of translocation (for reviews see, for example, Langlet 1971, Linhart and Grant 1996), why are there not similarly many reports of genetic mismatching affecting planting project success? There are several reasons for this lack of case studies. First, as just described, the expression of maladaptation may only occur over a very long time and many planting projects may not yet have shown perceptible signs of maladaptation. Over very long time periods, changes in management personnel and potential loss of records increase the likelihood that the reason for the failure will not be recognized. Second, providing proof of poor genetic matching requires that accurate and specific records have been kept both for the history of the introduced material and for the project site. Often, that information is not available. Although in some cases plant failure from maladaptation can be inferred by certain "genetic forensic" studies, the ability to provide such evidence is dependent on a number of factors. The introduced plants would need to be tied back to their source by comparing their genetic composition with that of other populations, and genetic differences between the introduced plants and the previous local population would need to be demonstrated. In some cases, there may be no existing genetic materials from the previous, local plant population. In any event, because typically there is not just a single known gene that is responsible for the maladaptation, there is usually inference involved in determining that the genetic differences between the original, local population and those that were introduced constitute differences in adaptation. More simply, genetic differences in themselves do not constitute proof of maladaptation of the introduced plants. Additional information usually gained from long-term garden studies and from hybridization studies is needed to demonstrate the relationship between genetic differences and adaptations to certain environmental conditions. Those studies, unfortunately, are largely lacking for most native plant species.

Genetic forensic studies themselves are vulnerable to the sampling design, techniques employed, and array of genetic diversity that may or may not yield clues for genetic differences. For example, there was interest in determining the genetic origin of a stand of ponderosa pine on the Idaho Panhandle National Forest. The stand has been used as a seed production area (SPA) for artificial regeneration projects on other sites. However, the origin of the stand—whether it is the result of natural regeneration following a fire or was artificially regenerated from a different source—is unknown. Samples were collected from both the SPA and from other possible native and non-local seed sources of ponderosa pine. Both allozyme and (chloroplast) DNA analysis were conducted. However, the results were inconclusive: while the results did not rule out a local origin for the stand, they could not provide conclusive evidence (Wilson and Hipkins 2000, Mahavolich and Hipkins 1999). The likelihood of having a conclusive result in these cases is influenced by the ability to clearly identify comparison stands that are genetically local and others that are non-local, to sample a sufficient range and number of trees per stand, and to determine a sufficient number of variable gene loci that differ between local and non-local sources.

Finally, the failure of a planting project may often be the result of several factors. The way the seeds or seedlings were handled or grown, stresses during transportation and planting, and subsequent site management all impact the survival and ensuing success of the plants. Even if the genetic material used in the project is well matched to the site, there can still be failures because of the nursery or management practices and their interaction with environmental conditions. For example, even well-adapted seeds could fail if planted at the wrong time or if site preparation is poor. So even if there is a failure in a restoration project, and it can be proven that the plant materials used are not local or are genetically different from the previous plant population that resided on the site, that still does not constitute proof that the main reason for the failure is genetic mismatching. For example, if genetically appropriately tree seedlings are introduced that are resistant to a particular pathogen, but there are other stresses (such as incorrect planting practices like a j-root), the poor planting can result in the seedling being too stressed to survive in the presence of the disease.

Regardless of the strenuous burden of proof in determining that a restoration or revegetation failure is due entirely or in part to genetic mismatching, there is considerable evidence from a combination of experimental studies and restoration plantings that meets the standard of "common sense". Within this evidentiary pool, we can consider four categories of information:

1. Case studies of plantings that have failed or have shown signs of potential failure, and there is reason to believe that one of the main reasons is genetic mismatching.

2. Case studies of controlled situations where plants with different genetic sources show differences in survival, growth, or reproduction in different environments.
3. Studies of specific genetic relationships or adaptations that if disrupted or undermined would have likely negative consequences.
4. Case studies of revegetation or restoration projects where the genetic source of the introduced plants is either unknown or is known to be non-local. These are cases where there is potential for maladaptation, and can be followed over time.

Examples of consequences—in theory and in practice

1. Failures or signs of reduced viability in planting projects related to genetic source. Many factors influence the initial survival and long-term success of a planting project, so it is often difficult to determine the contributing or main causes of failure. Signs of lower (than resident plant populations) fitness or lack of adaptation—may only appear after a long time. Suspected cases of maladaptation of introduced plant materials often remain speculation. Even if there is no direct proof, the speculation has considerable credibility if the introduced populations are far distant or very different (from the planting site) sources. One such case is illustrated by the large-scale fires in San Diego County, California, in 2003. These fires were fuelled by many dead trees, particularly pines, that had succumbed to a combination of drought and bark-beetle infestation, the latter probably a secondary effect of the drought rather than a major direct cause of mortality. Some of the affected area had been planted in the 1950s. The southern half of Cuyamaca State Park burned in 1950 and many pines were killed. The State, together with the Forest Service, initiated a program of replanting 200,000 seedlings of Coulter, Jeffrey, and Ponderosa pines over 5,000 acres. The State Park report for this project indicates that the genetic sources for the pines (including some broadcast seeding) included some local (collected within Cuyamaca State Park) and some non-local ("northern California") sources. The exact proportion of local and non-local pines that were introduced or that survived is not known. The use of non-local genetic sources is an understandable and perhaps common occurrence when there is a need to quickly produce a large number of seedlings. During the past decade, as annual precipitation had been below average, many, but not all, of the trees in Cuyamaca State Park were invaded by bark beetles. Thus, there is credible speculation that the infected, standing dead trees may have been those from northern California gene pools, which are less-adapted to the drier conditions of southern California and less resistant to bark beetle infestation. This possible case of genetic mismatching has not been confirmed (as of yet) by genetic testing (Michael Curto, November 2003, pers.com.).

Inappropriate seed source has been considered the most likely explanation for widespread and severe dieback in three ponderosa pine plantations planted in the late 1960s to mid-1970s south of Pagosa Springs, CO. Although a pathogen (*Cenangium ferruginosum*) has been identified in the plantations, observations are consistent with this being a secondary impact, and not the primary cause of failure (Worrall 2000). Conclusive evidence of a genetic mismatch has not yet been obtained, complicated by insufficient records of the planting stock and lack of a suspected seed source with which to compare the plantation trees. Support for this type of forensic study would be provided by having a DNA database that characterized known ponderosa pine sources for planting materials. This would then provide a reference when a suspected source was not available. This type of database is under development at NFGEL, but its efficacy will depend on the ability to find genetic markers that can distinguish the various sources (Hipkins 2004).

A class of planting projects known as “mitigation-related translocations” have a modest track record, in general. These are projects that remove protected or special-status plant populations from one site and attempt to re-establish them on another site. The recipient site could either be pre-existing habitat or habitat that is simply deemed suitable for that species. These projects are often mitigation efforts required by environmental Acts and related to development projects that cause habitat loss, fragmentation, or degradation (Howald 1996). Although the reasons for the frequent failures are not often known, it is probable that some of those failures are related to poor genetic matching or too narrow a genetic base for the plant materials.

Because of the context of mitigation-related translocations, genetic issues are likely for several reasons. First, these cases have the added complication that the translocation site may not have been pre-existing habitat, but simply an area that is deemed suitable habitat. As such, the idea of choosing locally adapted material may be doomed from the start. Second, the plant species may have already lost considerable genetic diversity as a result of its habitat loss or other impacts, and thus the source population(s) may be genetically deficient. Long-term monitoring studies that would have tracked these genetic changes and alerted restoration practitioners to deficiencies in genetic diversity are rare (see Box 9). Lastly, collection of genetic materials may occur very quickly as a result of a development schedule rather than on a schedule that optimizes genetic diversity or establishment success. Consequently, the sampling may not be adequate to represent sufficient and appropriate genetic diversity. This can occur when plant species with soil seed banks are sampled with just one attempt at collecting from the soil surface by raking or vacuuming. In those cases, the collection represents only a fraction of the genetic diversity in the soil seedbank that took multiple years to develop (Howald 1996).

Concern has also been expressed about the potential for genetic contamination from using state-listed plants in landscaping projects and even some restoration efforts. Such usage is apparently common, even though commercial distribution of endangered or threatened plants within the state in which they are listed is illegal, as the laws are not often enforced and the plants are widely distributed by commercial nurseries and other distributors (Reinartz 1995). If the appropriate seed source is not used, there is potential for the few remaining native populations of these species to be negatively influenced by gene flow from the introduced plants.

Translocation as a mitigation measure does not have a good record of success in California: of 45 translocation projects (established between 1983 and 1989) that were reviewed for status, only five were declared successful (Fiedler 1991). And all but one of those five were less than 20 years old, so long-term success or ongoing, viable natural regeneration and maintenance of biological diversity, has not been demonstrated even for those projects initially declared successful.

An example of mitigation-related translocation where lowered fitness and imminent planting failure has been connected with genetic issues is provided by a common coastal marine plant of California, eelgrass (*Zostera marina* L.). In southern California, it has suffered considerable habitat loss and fragmentation by dredging and other development-related activities and consequently there have been many transplantation projects. Although current transplantation protocol prescribes collection of plant material from the bed nearest the transplantation site, in many cases there may be no similar sites. It has been revealed by genetic analyses that the transplanted eelbeds have significantly lower genetic diversity than natural, undisturbed beds (Williams and Davis 1996). This could be the result of using too few genotypes to establish the new population—a situation exacerbated by the fact that the species can reproduce asexually as well as sexually, and thus sampling from different individual donor plants does not guarantee genetic diversity in the sample. There is concern that the low genetic diversity in the transplanted eelgrass beds might undermine their sustainability (Williams and Davis 1996). Moreover, subsequent studies showed that the loss of genetic diversity in the restored populations corresponded with lower rates of seed germination and fewer reproductive shoots, suggesting negative consequences for the restored populations (Williams and Davis 2001). This is a case where the amount of genetic diversity, rather than local adaptation, is the more critical issue. It is also possible that locally adapted material is not always used in restoration projects, as there is very little known about the genetic structure or local adaptations of the species.

Translocation studies have also been used to reveal the fate of hybrids that result from crossing between different populations or subspecies of native plants. In reciprocal transplant experiments in Utah for two subspecies of Big sagebrush —Basin big sagebrush ((*Artemesia tridentata* Nutt.) ssp. *tridentata*) and Mountain big sagebrush (*A.t.* ssp. *vaseyana*)—and their hybrids, it was clearly demonstrated that each subspecies was more fit than either the other subspecies or their hybrids when growing in its natural environment. (In Utah, the two subspecies grow at different elevations, with a narrow natural hybrid zone at the interface.) The relative fitness (a composite index that included seedling survival, percentage of seedlings that flowered, number of seeds per seedling, and seed germination rate) of the basin big sagebrush in its own environment (below 1777 m in elevation) was approximately 10 times that of the (normally growing above 1879 m elevation) mountain big sagebrush growing in the same (lower elevation) environment (Wang et al. 1997).

2. Case studies of controlled situations where plants with different genetic sources show differences in survival, growth, or reproduction in different environments. Transplantation studies—such as that classic series by Clausen, Keck, and Hiesey (1940) described in Chapter 6—or provenance studies are good demonstrations of what will likely happen if seed sources of various species are used in situations that differ significantly from their natural environment. There are many such examples for forest tree species in particular, because of the long history and experience of planting forest trees after fires or harvests, because of their commercial value, and because of their often-high levels of genetic diversity that is usually structured geographically (Millar and Libby 1989). Just a few examples will be given here, as this general class of studies is described in more detail in Chapter 6.

Because of its extensive geographic range, a rangewide provenance test of black walnut (*Juglans nigra* L.) offers dramatic evidence of consequences of making bad genetic matches. Its natural range extends from the eastern United States west to Kansas, South Dakota, and eastern Texas. A subset of 15 to 25 sources from sixty-six sampled provenances were planted in each of seven geographically disparate common-garden plantations. After 22 years, survival of local trees (within a 100-mile radius of the plantation site) at the three northern plantations (Iowa, Michigan, and Minnesota) was much higher than for the other provenances. Differences at the more southern plantations were less extreme. At the Minnesota plantation, several provenances from Kentucky, Virginia, and Tennessee had zero survival, while the local provenance had 71% survival. The findings resulted in the authors' recommendations to use local seed sources to regenerate extreme northern and western areas of the walnut's range (Bresnan et al. 1994).

Switchgrass (*Panicum virgatum* L.) is a geographically widespread perennial grass species east of the Rocky Mountains that currently exists in many remnant prairie sites as well as cultivated or managed areas. In addition to covering a wide latitudinal range, it also has distinctive types described as upland and lowland ecotypes that differ in ploidy level, habitat preference, and some molecular markers. Upland ecotypes, which are generally hexaploid or octoploid, occur frequently in drier sites. Lowland ecotypes, which are commonly tetraploid, are generally found in wetter environments. Samples from twenty native populations (including locations in Kansas, South Dakota, and Nebraska) were planted in common-garden studies in five diverse locations in 1998. There were significant interactions between population source and plantation site for survival and growth characteristics, indicating a strong role of latitude in determining response. For example, moving a southern latitude/upland population approximately 2 degrees north resulted in a 9 to 17% decrease in survival (Casler et al 2004). The study results are evidence of adaptation related to temperature patterns, growing season, and upland-lowland characteristics and are evidence of certain failures or lowered survival if seed sources of switchgrass are moved between upland and lowland conditions or across latitudinal differences of even 2 degrees. Because latitude and habitat preference are somewhat inter-related within the species' range (that is, the species is not found at its full habitat range across its full geographic range), these effects can be completely assessed independently. As such, a cautious application of these study results is to only use plant materials that closely match the planting site in ploidy level, habitat type, and latitude.

Big sagebrush is similarly a widespread species, dominating over 150,000 km² of landscape in the Great Basin region. Consistent with the environmental variation encompassed by its natural range, the species has three recognized subspecies: *A.t.* ssp. *wyomingensis*, ssp. *vaseyana*, and ssp. *tridentata*. These subspecies not only differ morphologically in size, inflorescence structure, and ploidy level, but common-garden studies have revealed substantial genetically based differences in drought adaptation. Although there are only two ploidy levels (diploid and tetraploid), making it difficult to determine a strong correlation between ploidy and other characteristics, there is a general relationship that the tetraploids are better adapted to dry conditions than the diploids (see Figure 7.1) These adaptations reflect the range of the species' natural conditions from low elevation and driest conditions (ssp. *wyomingensis*) to the higher elevation, more mesic conditions (ssp. *vaseyana*) (Kolb and Sperry 1999). These genetically based differences in morphology and physiology would be predicted to undermine long-term survival if the subspecies were planted well outside their respective normal range of environmental conditions.

Another geographically widespread species, *Chamaecrista fasciculata* Michz., also shows adaptive variation, but only at long distances. This predominantly outcrossing, annual legume grows in disturbed sites over much of eastern North America, including Kansas and South Dakota. Common garden studies with transplanted materials showed that survival, fruit production, and other fitness-related characteristics were often reduced when the transplant distances were long—generally over 2,000 km (Galloway and Fenster 2000). Seed collected in Illinois and used in restoration plantings in Kansas might be expected to show signs of maladaptation.

3. Studies of specific genetic relationships or adaptations that if disrupted or undermined would have likely negative consequences. There are many examples of intricate interactions—especially between plants and insects—where association is specific with particular populations (Breedlove and Ehrlich 1968, Longcore et al. 2000). There is strong evidence of co-evolution between particular populations of a lupine species (*Lupinus amplus* Greene) and a small lycaenid butterfly (*Glaucopsyche lygdamus*) in Colorado. In one lupine population near Gothic, CO (latitude 38° 57′ 34.9; longitude 106° 59′ 22.7), the plants are severely browsed by (certain life stages of) this butterfly species and, over time, the plants have responded (via selection) by having an earlier flowering time, thus minimizing insect damage by having the flowers mature before the adult butterflies emerge. In contrast, in the lupine population just five miles away at Crested Butte, the butterfly is rarely seen and the lupines have a later flowering time (Breedlove and Ehrlich 1968). This is one example of how using an inappropriate genetic source can have consequences that go beyond the introduced species itself, and extend further into the ecological community.

Differences in ploidy levels within a plant species represent another category of specific compatibilities that if disrupted—by planting or seeding incompatible mating types—could represent major planting failures. The previously mentioned switchgrass—a cross-pollinated perennial—has ploidy levels from diploid (2n=18) to duodecaploid (2n=108). Tetraploid and octaploid plants are the most abundant in nature and are often found in the same native prairies, but hexaploids are rare. Controlled studies have shown that switchgrass plants produce very little or no seed when self-pollinated (Talbert et al. 1983). More recently, reciprocal crosses performed between tetraploid and octaploid switchgrass plants revealed substantial mating incompatibilities between them. Poor seed set and other seed traits were observed with inter-ploidy crosses, and both pre- and post-fertilization incompatibilities were noted (Martinez-Reyna and Vogel 2002). Taking into consideration that switchgrass is an obligate outcrosser together with the mating incompatibility between plants with different ploidy levels (cytotypes), restoration failures could be predicted if the source and resident populations are not screened for cytotype and if the correct cytotypes are not planted. Screening for ploidy level is fairly routine now. Such services are available from the Forest Service’s National Forest Genetics Laboratory (NFGEL), USDA, Placerville, CA and other research institutions with flow cytometry capability. See Box 14 for more information on genetic considerations for polyploidy plant species.

4. Cases of known or suspected genetic mismatches—consequences pending. There are no doubt more examples of genetic mismatches in planting projects than of planting genetically appropriate materials. This is easily understandable as information has been only slowly and recently available to guide any such decisions except those involving commercial forest tree species. A sense of urgency in some planting projects often outweighs genetic considerations, and appropriate genetic materials cannot be collected and multiplied in time to meet the demand.

In 1994, a commercial variety of mountain brome (*Bromus marginatus* Nees ex. Steud.) was planted at approximately 10,000 ft. elevation on Forest Service land on Crested Butte Mountain, Colorado. The seed source for the variety, called ‘Garnet’, is in Granite County, Montana, near the ghost town of Garnet, elevation 5,900 ft. Subsequent monitoring has revealed that the brome doesn’t grow to a height of more than 6 to 7 in. on the Crested Butte Mountain site, nor has it flowered. The genetic concern here is that there is native mountain brome on the same mountain. It typically grows to 36 in. in height, flowers, and sets seed. Although the introduced brome would appear to be ill-adapted to this site given the difference in elevation from its genetic source, there is still potential for genetic contamination of the local brome populations if there is even a small amount of seed production, perhaps the result of an unusual weather pattern that provides temporary conditions sufficient for seed production (G. Austin, pers. com. April 2004). At least it shouldn’t spread vegetatively as the species doesn’t have rhizomes (A. Kratz, pers. com. April 2004).

Planting projects involving non-local cultivars of the perennial prairie grasses big bluestem (*Andropogon gerardii* Vitman) and Indiangrass (*Sorghastrum nutans* (L.) Nash) potentially have genetic consequences for native tallgrass prairie remnant sites. Both grasses are polyploids and self-incompatible: Indian grass is a tetraploid and big bluestem is a more complicated higher order polyploid, with two cytotype races (types with different ploidy levels). These ploidy differences add to the risk of using inappropriate genetic sources for planting projects, as mating incompatibilities are more likely. Studies that have compared the genetic diversity of several cultivars of these species with both native remnant and restored sites, reveal that while the *amount* of genetic diversity in the cultivars can be similar to that of the native remnants, the *nature* of the genetic diversity can be quite different. Genetic differences were revealed between native remnant grasslands of these co-dominant species in Illinois and in Kansas, and between the native remnants and all the cultivars. (Cultivars studied for big bluestem were from Iowa, Nebraska, and Kansas, and those for Indian grass were from Illinois and Oklahoma). In these cases, the concern seems to be more about the consequences of using possibly poorly adapted material, rather than using genetically restricted cultivars. Seeding of these two species has occurred widely in North American prairie restorations, as cover crops to reduce soil erosion and as a native forage crop for livestock. The potential for genetic mismatches using distant-source cultivars is high. Although the genetic consequences for the native remnants have not be directly studied, there are potentially serious consequences based on the genetic dissimilarities between distant populations, coupled with evidence of differences within these species (that is between populations or ecotypes) in mycorrhizal associations and competitive abilities (Gustafson et al. 2004).

Making genetically appropriate decisions for planting materials at the urban-wildland interface can be just as important as for natural areas. Following the October 20, 1991 fire in the hills of Berkeley and Oakland, CA, non-local seed sources were used for several native plant species. For example, seeds of the California poppy (*Eschscholzia californica* Cham.)—a widespread species with high regional genetic variation—came from a nursery in Oregon and were almost certainly non-local to the planting site, and the source for blue lupine (identified in the planting project only as to genus—*Lupinus* sp.) was somewhere near Lompoc, in southern California. Through the intervention of local forest geneticists, however, the project managers were convinced to wait several years to replant with appropriate sources of coast redwood (*Sequoia sempervirens* D. Don), allowing time for local seed collections and seedling development (Libby and Rodrigues 1992). Waiting for genetically appropriate planting materials to be developed, however, is not always a managerial option.

Consequences are not always reciprocal

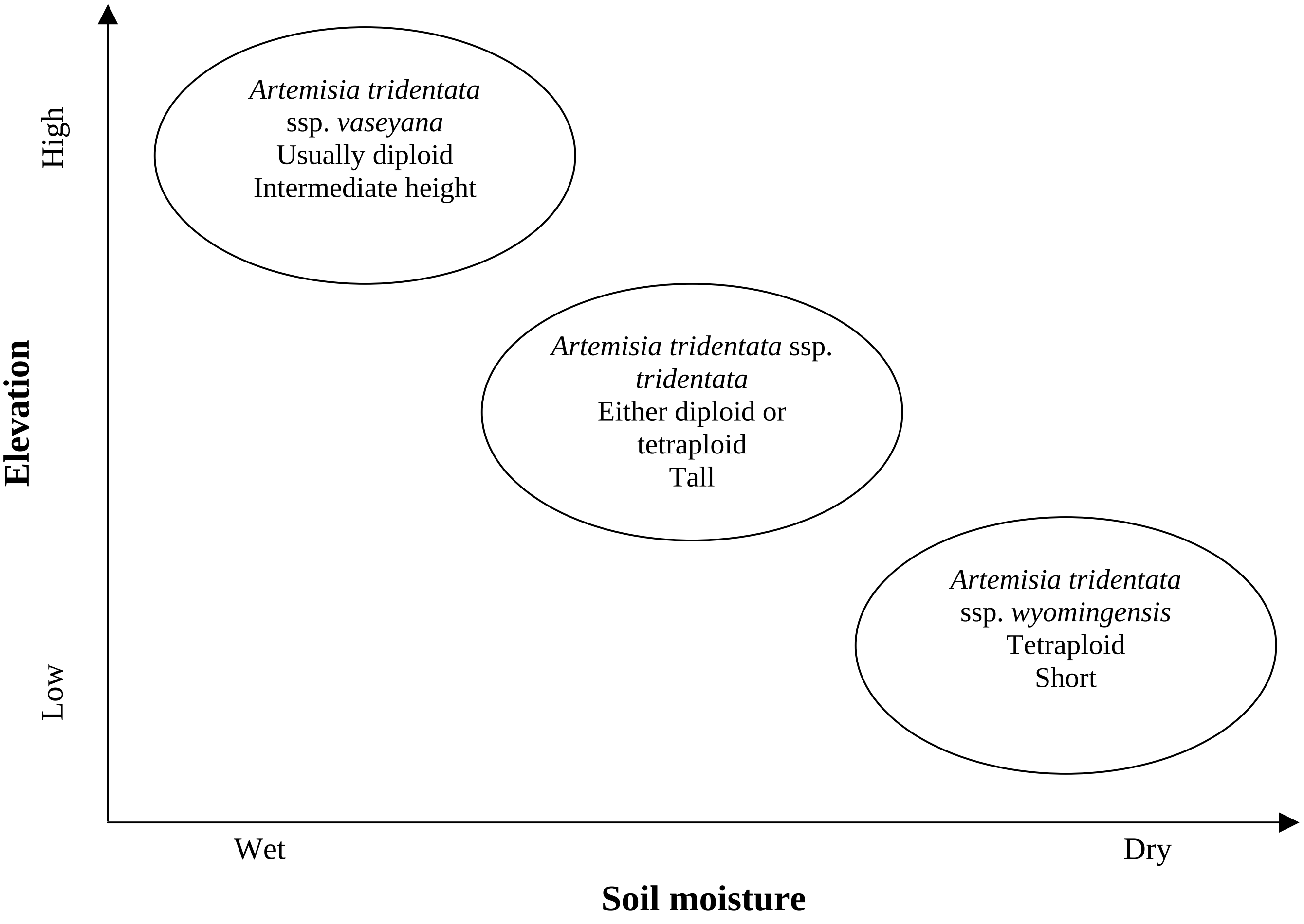
Common outcomes from provenance and transplanting studies are that the negative effects of introducing non-local plant populations may not be completely reciprocal. Often, moving plants in one direction (such as moving southern seed sources north) does not have the same effect as the opposite movement (moving northern seed sources south). This same observation is often made in studies that move plants from different elevations along an elevation gradient. The reasons for this lack of reciprocity seem intuitive: adaptations to some environments (such as cold tolerance) may still not preclude survival in other (warmer environments), while the opposite may not be true. So not only is the degree of impact, or severity of consequence, of genetic mismatching not directly related to the amount of geographic distance in all cases (as species differ greatly in the spatial scales on which they show local adaptations), but it can also depend on direction of change—literally, or with respect to some environmental feature.

Such non-reciprocal effects may be expressed not only in survival and growth, but frequently in mating success (see Stebbins 1958a). A case in point is provided by two subspecies—a coastal and inland ecotype—of gilia (*Gilia capitata* Dougl.) in California. The two ecotypes have some distinct morphological differences. In addition to providing evidence of local adaptation with common-garden studies, it was determined that the coastal ecotype could not successfully fertilize the inland ecotype's seeds whereas fertilization in the other direction was possible (Nagy 1997).

Concluding notes

The consequences of choosing a genetically inappropriate source for planting projects can have a broad spectrum of consequences –from severe and lethal, to lesser degrees of impact on fitness. The consequences can be immediate, and limited to the plants introduced, or they can spread to neighboring native plant populations if the introduced plants survive to the reproductive stage. Real examples of genetic mismatches are difficult to find as they require both strong scientific evidence of local adaptation and records of the seed source used in the planting project. Where there is an obvious planting failure, genetic mismatching may be just one of many putative causes of the failure. In any event, good record-keeping for (genetic) source for all planting or seeding projects is useful in learning more about local adaptations of native plant species and better understanding the likely causes for both successes and disappointing results.

Figure 7.1. The three subspecies of *Artemisia tridentata* in relation to the habitats to which they are adapted. Adapted from Kolb and Sperry 1999.



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Box 8: Making the Best Use of Limited and Valuable Genetic Collections

Collections of plant genetic materials—called *ex situ* collections after being collected and stored offsite—are made for various reasons. These include direct restoration or revegetation, *ex situ* conservation (longer term storage in case of the need for restoration of native populations)—especially of threatened or endangered species, research, parent materials for multiplication, and educational purposes. Government agencies, nonprofit organizations, individual researchers, and private companies are entities that have typically been involved in *ex situ* collections of plant materials for one or more of these reasons. For the Forest Service, *ex situ* seed collections are particularly important because of catastrophic events, such as fires or insect or disease epidemics, that may increase demand beyond supplies that could be quickly available from new collections. Examples of situations where the need for seed for restoration purposes overwhelmed the current availability include several National Forests in southern Colorado after the 2002 fires. *Ex situ* collections of plant materials—including how to sample the source populations, techniques for storage, legal issues, and other related topics—have been the theme of many symposia, workshops, books, and papers (see Guerrant et al. 2004 for a review of topics related to *ex situ* conservation of native plant species).

For some native plant species, particularly commercially valuable forest tree species, *ex situ* collections were used to establish breeding orchards and seed orchards in some locations. This has allowed the opportunity not only for scaling up the germplasm for those populations over time, but for selection of certain kinds of characteristics so that the planted generation has been shifted towards what was considered a more desirable tree phenotype. In the Forest Service, standard operating procedure for plant species in genetics programs, including Region 2, are collections for the primary purpose (such as seed orchard establishment, progeny testing), plus a minimum of 300 seeds from plus-trees for gene conservation (USDA Forest Service 1993). In Regions 1 and 4, pollen collections are also required—a minimum of 10 grams of pollen per elite tree (superior tree identified from progeny testing) (M.F. Mahalovich, pers.com). With a change in emphasis towards considering all plant species in the ecosystem rather than just the commercially significant species, and towards protection of biodiversity and ecosystem health, a similar strategy has been suggested for other native plants. However, because less is known about the requirements for stratification, sowing, germination and long-term storage for these noncommercial species, it may be advisable to collect a higher number of seeds (M.F. Mahalovich, pers. com.). As part of this trend towards managing for a broader suite of plant species, the National US Forest Service Tree Seed Lab in Dry Branch, GA recently expanded their mission to include other native plants (M.F. Mahalovich, pers. com.).

The existing genetic collections of native plant populations are often limited in supply. Although scaling up the material may be an option, this can require considerable time for some species. If the species is restricted to sexual reproduction, this places more limitations on multiplication of the genetic collection than is true for species that can be vegetatively propagated. In either case, there are genetic implications of scaling up the genetic collection: see Chapter 8 for more information on that topic.

The seed supply may be limited for several reasons: seed may be available in native populations but has not been collected sufficiently to produce a good supply; seed may be only sporadically available in native populations; seeds may be difficult to collect from the wild; the species may be threatened or endangered and seed is only available in short supply even in the wild; seeds of the species may have a short shelf life and have to be collected prior to any anticipated use. The *ex situ* collection may not be completely replaceable because the genetic source may be gone, depleted, or contaminated. For example, the collection may represent some populations—and attendant genetic diversity—that is no longer available in natural populations because of their extirpation. In those cases, it is appropriate to treat *ex situ* collections as valuable and finite. Use of these collections should be guided by a policy that considers the value of the proposed use and the benefits and risks of reducing the *ex situ* collection for this purpose.

In general, finite and valuable germplasm collections are best supported by maintaining them under species-specific storage conditions. Different species have different shelf-lives for their seeds (from less than a year to decades), but these times can be extended with storage conditions that address the particular seed chemistry of each species. Appropriate storage protocols are important not only in preserving the amount of seed, but its genetic integrity. Storage methods can act as an additional selection agent, favoring some genotypes over others, and thus shift the range of genetic variation over time in the seed collection. The USDA's National Center for Genetic Resources Preservation can be a useful resource in determining the best long-term storage conditions for various species. Their research activities are helping to develop tools to expand gene banks' capacities to assess and efficiently capture genetic diversity, to enhance longevity of stored germplasm, and to improve tools that validate and predict viability and genetic integrity of accessions (http://www.ars-grin.gov/ncgrp/). In some situations—especially with rare or exceptionally valuable genetic material, it may be appropriate to apply some of the newer technologies. These technologies include cryopreservation for long-term storage (see Engelmann and Engels, 2002, for a review of storage methods), and methods of cloning the embryos (see, for example, Hargreaves et al. 1999). Although this wouldn't increase the genetic diversity of the collection, it would provide better risk management of the collection by allowing copies of genotypes to be maintained at several storage sites, and it would allow multiple uses (for example, research and restoration) of the same genotypes. In all cases, maintenance of the identity of limited genetic material is critical.

If the *ex situ* genetic collection is not a product of nursery multiplication or otherwise replaceable, the best use of this material should be considered before committing it to a use. This principle applies regardless of whether the seeds come from a Plant Materials Center, are collected by Forest Service personnel, are collected by a contractor, or other origin. When the potential purpose for the genetic collection is a restoration project, some parameters to consider in making the decision about the best use of limited material include:

- Is natural regeneration likely? (More emphasis should be given to situations where natural regeneration is highly unlikely).
- Is the seed (or other) collection genetically appropriate for the restoration site? (If so, this goes in favor of this use of the genetic material. If not, there is a risk of genetic contamination to neighboring plant populations (if they exist) and increased risk of project failure because of possible lack of local adaptation.)
- Can the material be scaled up in an appropriate manner (see Chapter 8) and time period to serve the restoration objective?

Sometimes a genetic collection, or portion thereof, is requested for research purposes. Research can be a high priority, particularly if there is little genetic information currently available with which to guide conservation or restoration efforts. However, the nature of the research should be carefully considered in determining whether this is a high-priority use of limited genetic material. The table below provides some rationale for determining whether a limited seed collection is best used in a research capacity.

In addition, some manner of financial or inkind contribution could be considered if public-domain genetic collections are used for research. Financial support is often a limiting factor in long-term conservation of *ex situ* genetic collections. Genetic collections are particularly concentrated in the public sector and are disproportionately affected with government cutbacks in budgets. The true value of genetic collections has not been calculated or internalized in activities—such as research—that make use of them (Hoagland 1996). To mitigate this problem, pricing schedules could be developed to suggest financial contributions by researchers who use public-domain genetic collections—particularly those that are irreplaceable or otherwise high value. These expenses could become normalized in research proposals. Contributions received from researchers in recognition of the value of plant collections will provide more resources for further collections and long-term conservation. Regardless of any policy restrictions concerning reimbursement for genetic collections, even the act of placing a value on the collections can be important: communicating to researchers the need to use alternative material if this doesn't undermine the objectives and to make the research methods as parsimonious as possible.

In some regions of the Forest Service, including Region 2, seed procurement plans are part of the normal operating procedure (USDA Forest Service 1993). These ten-year plans are meant to provide for adequate supplies of seeds for normal operational purposes as well as revegetation projects associated with catastrophic events. Although these plans currently refer to forest tree species only, there may be interest in developing this management approach for other plant species in the future.

In summary, unless genetic collections are confidently replaceable, their best use should be considered before spending that resource. All collections have costs, regardless of how they are paid, and some collections may not be replaceable. Consequently, there may be both a direct cost and an opportunity cost in using a genetic collection. As indicated in Chapter 1, one of the consequences of using genetic material inappropriately (such as not matching them well to a project site, with subsequent plant failure) is the waste of genetic resources that are valuable and perhaps irreplaceable.

Table B8.1. Spectrum of value to be applied to research projects that requests use of limited collection of plant genetic resources. (Adapted from Table 12, Rogers 2002.)

Higher value	**Lower value**
Research is novel	Research is redundant
Research methods are efficient, not wasteful	Methods unnecessarily consume germplasm
Objectives require specific genetic material	Objectives could be satisfied with less valuable genetic collections or new collections
Outcome likely to support conservation of species	Research has little or no conservation or restoration application
Germplasm or DNA products can be reused for other purposes	Germplasm is completely consumed or contaminated by the research

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Box 9: Genetic Monitoring for Signs of Genetic Erosion or Genetic Shifts in Natural Settings

The intended meaning here of the term genetic monitoring is the use of genetic analysis, usually over more than one plant generation, to detect changes in genetic diversity of a resident or introduced plant population in a natural setting. In absolute time this can be over a very long period for long-lived plants, or over a relatively short time for many forbs and grasses.

A different but common interpretation of this term is monitoring for symptoms of adaptation or maladaptation of plants that have been introduced to a site for reforestation or restoration purposes. In addition, seed collections in seed bank facilities, propagation material in nurseries, and other genetic collections may be monitored to note changes in genetic diversity over time. That situation is described in Chapter 8. Here, the focus is on plants in natural settings. And still another type of genetic monitoring is evaluating nursery cultural practices. For example, if the genetic diversity of the parent plants is known, then reductions in genetic diversity of the resulting seedlings that are available for revegetation projects can be inferred to be the result of selective culling, seedling grading, other practices that can reduce diversity. If seedlings are selected for uniformity, or for particular traits (such as fast growth), genetic diversity may be reduced and other important traits may be lost or lowered in frequency.

Changes in genetic diversity, to some extent, are normal. Genetic diversity is very dynamic—changing in response to both natural and artificial influences. Genetic change may be a pathway to adaptive change, to speciation, to extinction, or it may be a random fluctuation. This means that monitoring changes in genetic diversity must be firmly based in a biologically meaningful context: it is important to be able to interpret whether the changes are within a normal or desirable range, or whether they might signal some serious loss that could have negative repercussions for the species as a whole or a portion (segment) of their populations.

Repeated genetic studies—genetic monitoring—are necessary because undesirable genetic change can usually only be determined in the context of a genetic trajectory or in relation to baseline genetic information prior to the impact or influence of concern. Timeframes for monitoring and plotting trajectories are usually related to a generation of the species of interest rather than a standard unit of time. A 10-year planning horizon would be consistent with genetic monitoring for some species (annuals), and not for others (long-lived trees or shrubs). Baseline data and long-term monitoring are usually required to detect subtle changes resulting from gradual losses in habitat or climatic change. These data could include measures of heterozygosity, frequency of rare alleles, or other diversity measures (see Chapter 4). However, genetic information can be gained in some situations within shorter time spans—even several years. Examples of these situations include sudden die-offs due to catastrophic events such as severe drought, volcanoes, chemical spills, etc. Genotoxic chemicals cause damage directly to genetic material and can be directly measured in structural changes in the DNA or effects on processes involving DNA. Genotoxic damage if not repaired, may result in genetic change in the form of mutations (Belfiore and Anderson 1998). But even changes in allele frequencies can occur quickly. Other situations where changes in genetic diversity may appear quite rapidly include seedlots that have been increased over several generations in a nursery from only a few parents, or from parents that otherwise do not reflect the diversity in the native population (that is, poor sampling criteria). See Chapter 8 for more discussion on the latter two situations.

Genetic monitoring is not routine for plant populations in natural settings, and is more usually limited to a few studies that may track a change rather than a long-term monitoring program. And often the situations involve listed species, comparing levels of genetic diversity in a plant population or region before and after a disturbance. For example, one study demonstrated loss of genetic diversity in the perennial herb, Mead's milkweed (*Asclepias meadii* Torr. [Asclepiadaceae]) (federal- or state-listed as threatened), as a result of mowing. Mowing of this plant in its tallgrass prairie ecosystems in Kansas and Missouri increased the ratio of vegetative to sexual reproduction, lowering genetic diversity (Tecic et al. 1998). Because of the resources required it is not realistic to undertake genetic monitoring for a large number of native plant species. Instead, it is reasonable to develop criteria to select a few species or situations that might particularly benefit from genetic monitoring, or otherwise provide meaningful information. For example, Ellstrand and Elam (1993) suggested that warning signs that plant species or populations might be particularly vulnerable to human-caused disturbance might include changes in population size, degree of isolation, and fitness. More generally, selection criteria for monitoring activity might include:

- Species or populations that have recently undergone a major disturbance affecting their census or habitat size;
- Those with some existing baseline genetic data;
- Those that are known or suspected to be particularly sensitive to human influences or climate change, geographically restricted species;
- Federal- or state-listed species.

Species characteristics affect the type of genetic monitoring that is possible or practical. Species with long individual lifespans and many overlapping generations (for example, *Sequoiadendron giganteum* (Lindl.) Buchh., giant Sequoia) can be simultaneously sampled for genetic change over those generations. In addition, different types of genetic variation may respond to influences at different rates and magnitudes. For example, after going through an extended bottleneck that reduces population size and genetic diversity dramatically, genetic variation in selectively neutral traits may require many thousands of generations to recover whereas recovery of variation for adaptive quantitative traits may require only hundreds of generations (Milligan et al. 1994).

Genetic monitoring could track several genetic characteristics such as major shifts in critical genes, simple losses of genetic diversity, changes in the effective population size or heterozyogosity, or other measures. None of these provide comprehensive information on the nature or consequences of the genetic change and all require a well-designed study. As an example, consider monitoring for a loss of genetic diversity—with losses over a certain level acting as a signal for concern. This application has many caveats. First, determining normal ranges of variation for species and populations within species is complicated and resource-demanding. Second, interpretations vary depending on species characteristics. Species that can reproduce both sexually and asexually may show fluctuations in genetic diversity as a function of the ratio of sexually- versus asexually-derived recruits over time. Furthermore, losses in diversity in this situation do not necessarily suggest loss of adaptability and gains in diversity do not necessarily represent improvements in adaptive ability because these measures are descriptive measures.

There are some cases in which monitoring genetic diversity can provide evidence of a species in trouble even before there are demographic consequences. One such situation is a recent bottleneck. Bottlenecks could go undetected in traditional demographic monitoring where census or survey methods have low statistical power, in situations with high variance in family size, and when there are few breeders of one sex due to a skewed sex ratio or a breeding system that favors individuals of one sex mating with many of the other sex (Luikart et al. 1998). Early detection is important to avoid the potentially harmful effects of bottlenecks. This is particularly important for threatened species (Lande and Barrowclaugh 1987). Methods have been developed that can help elucidate a recent bottleneck, even after only one generation. Samples of the population, taken at least one generation apart, are compared for variance in allele frequencies. This variance test has been determined to be a powerful measure of a recent bottleneck (Luikart et al. 1998). Specifically, it has been shown to be the most powerful of several genetic monitoring tests (including changes in the distribution of allele frequencies); its power remains high for loci with few rare alleles.

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Chapter 8

Purchased Plant Materials for Wildland Revegetation Projects

After large unplanned disturbances such as wildfires, seeds and other germplasm may need to be purchased for revegetation projects if natural regeneration is poor and USDA Forest Service seed supplies from an appropriate source are low. There is a wide array of native plant materials available for purchase and from other agencies within the USDA that may be considered for use. Evaluating their genetic appropriateness for different planting contexts can be difficult if one is unfamiliar with how commercial and USDA plant materials are classified and produced. Available plant materials include wildland-collected germplasm that has been unaltered by purposeful selection and unintentional selection minimized, scaled up or “field increased” seeds from plantings of wildland-collected seeds, releases of selected germplasm, tested germplasm, release germplasm, and cultivars that have been derived in various ways from wild germplasm (Figure 8.1, Boxes 10 and 11). Within any class of materials, there will be some that are more appropriate than others in the context of managing native biodiversity and others more appropriate for more domestic or agricultural uses. This chapter will examine potential genetic influences of different kinds of native plant materials that are commercially available. We focus primarily on the issues surrounding documentation and collection of wildland germplasm, seed increase, and attributes of native cultivars and other materials developed from native species populations. This chapter also discusses some of the potential problems associated with available plant material choices. Before delving into problems, we want to emphasize that there are many potentially useful and genetically appropriate native plant materials available, and more are becoming available each year. There is reason for optimism.

There are some potential risks to native plant populations and communities from the planting of purchased materials that may differ from germplasm collected by local Districts within the Forest Service. Often, the plant materials available in bulk have been cultivated in increase fields from accessions collected many years ago. Techniques of sampling and harvest or artificial (purposeful) selection may have significantly compromised genetic variation. Alternatively, multiple populations from wildly diverse areas may have been blended together. In Chapters 9-10, a series of guiding questions, principles, and plant data are presented to assist in making choices among germplasm source populations. In this chapter, a series of questions are provided to increase awareness about how processing of germplasm during plant materials development or commercial seed production adds another layer of potential influences on the genetics of populations.

The information and questions provided below are intended to assist the Guide reader in an evaluation of available materials keeping in mind the project context. The questions complement those considered in Chapter 9. Determining which purchased plant materials are appropriate will vary with the goals and competing elements surrounding a project. If the project goal is to restore a post-fire or post-harvest site to a native condition, local seeds and unselected germplasm will likely be most compatible with the existing native communities. If before disturbance the site was previously planted with off-site plant materials, or covered with a high density of aggressive invasive species, then less conservative choices, in the sense of similarity to native resident populations, may be appropriate. As explained in earlier chapters, some disturbances, such as those where soil structure and chemistry has been severely altered by mining, may require different plant materials than are appropriate for less drastic forms of disturbance. Sometimes the only plants that will grow are ones that differ from prior or neighboring vegetation. In such instances, perhaps nurse crops of specially bred, selected, or tested plant materials may be needed. However, Brown and Amacher (1999) argue that a diversity of natural species can handle most harsh situations. The information provided in this Chapter is especially relevant to revegetation post-fire and post-harvest, but it is also relevant to revegetation of road right-of-ways, mining sites, revegetation of retired roads, and riparian habitat restoration. Plant material releases are often used in these situations, especially road right-of-ways through National Forests and Grasslands. Road corridors, current or recently retired, serve as important dispersal corridors among many types of wildland habitat for both native and invasive species. For this reason, it is important to consider them in an ecological restoration context.

The genetic diversity and natural adaptation of plant materials can be affected during every stage of their processing from collection, to cleaning, to field increase, to storage. To insure that one understands the potential consequences of processing and the effects of a plant material, a series of questions can be asked about every germplasm considered for purchase. It may not be possible to obtain answers to all questions, but even incomplete information can help to assure the choice of appropriate plant material.

Of the eight questions below, the focus of this chapter is on the first six. Information pertaining to questions 7 and 8 is available in other publications, some of which are noted later.

1. How was the original germplasm collected and processed?
2. Were collection location and subsequent treatment well documented?
3. How might cultivation, selection, and harvest practices have affected genetic diversity?
4. Were releases tested for environmental impacts and risks to native populations?
5. If considered as a nurse crop, does a particular non-local release have attributes to prevent gene flow into native population or aggressive takeover?
6. Are there cumulative impacts from repeated extensive use of limited cultivars?
7. Were the seeds tested for viability, germination, and weed content?

8. How long has it been since seeds were collected and seed viability tested?

This chapter does not provide a detailed review of plant materials. Reviews on various aspects of this expanding field are readily available. The USDA Forest Service, Shrub Sciences Laboratory has been working on plant material development since its establishment in 1970. McArthur (1988) reviews the early development of native plant materials, and McArthur and Young (1999) provide estimates of the market supply and demand for native seeds. Monsen and Shaw (2001) provide a history of many aspects of plant materials development, including federal policy and the influence of shifting objectives. In addition, an internal USDA Forest Service publication on cultivars of native grasses, including their origins, development, certification, and use is being developed by the Pacific Northwest Region and the Native Seed Network (Aubry 2004). Vogel and Pederson (1993) review the breeding techniques used in the testing and selection of many cultivar releases. Stevens et al. (1996) provide information on forb and shrub plant materials and seed certification in Utah. Lippitt et al. (1994) cover the importance of site selection, harvest practices, seed processing, tracking, and storage techniques. Information about the origins and development of particular plant materials and releases is available at several websites (Englert et al. 2002, Native Seed Network 2004b, NRCS-PMC 2004). Additional resources are listed at the end of this chapter.

Background on terminology, certification, and recent positive directions

Terminology. The terminology associated with plant production used by USDA agencies and the seed industry have not always been the same. The Association of Official Seed Certifying Agencies (AOSCA) developed standards for classifying plant materials and documenting the collection location of original accessions in the 1990’s (Box 10, 11). Figure 8.1 shows the AOSCA classification scheme for plant materials available from the seed industry and the USDA Natural Resource Conservation Service (NRCS) Plant Materials Centers (PMCs). The figure indicates three classes of pre-variety germplasm under the “natural track.” These natural track seeds are the ones most representative of the natural parent population. The development of the different classes of natural track germplasm must follow the direction of the arrows. If at anytime the germplasm within the natural track is shown to shift significantly from that of the parent population, the germplasm is relegated to a class within the “genetically manipulated” category of germplasm. Thus, it looses its natural track status. Table 8.1 compares the major specifications and requirements for the release of these different kinds of materials by PMCs to the public. Further details about releases and classes of germplasm are in Boxes 10-11 and the USDA NRCS, Native Plant Materials Manual (NPMM 2000).

Certification. Collection, documentation, and tracking procedures for wild-collected seeds may differ among government agencies and private seed companies. Box 10 provides an explanation of “wildland seed certification” programs available to the private seed industry and to government agencies through state certification agencies. Knowledge of the basic system will help in the evaluation and choice of different plant materials.

The increased demand for native plant materials for conservation and restoration together with the availability of wildland-collected certification programs have resulted in a steady increase in the quantity and diversity of native species available for purchase (McArthur and Young 1999). This is in part due to the release of AOSCA certified pre-varietal germplasm from PMCs. For example, the Bridger PMC has supplied source-identified germplasm to private industry (M. Moore, pers. com.). A private seed company in Wyoming within Region 2 has been cooperating with the PMC and is producing yellow-tagged, source-identified seed releases for native planting projects (Wind River Seeds 2004).

National Forests in Region 6 have their own internal tracking system for native germplasm and don't normally use AOSCA seed certification unless a contract grower chooses to pursue certification. Certified seeds can sometimes capture higher value in the open market. National Forests are increasingly contracting directly with commercial growers for seed increase of specific germplasm. In the Pacific Northwest, for example, the Umatilla National Forest coordinates an interagency seed production contract that involves a pre-qualified pool of selected growers. Task orders .for specific species and quantities of seed can be issued by any National Forest or BLM unit in Oregon and Washington, and then competed among the growers for price (V. Erickson, pers. com.).

State seed laws vary among states including with regard to some of the provisions of seed certification. Because of local differences in seed law and seed certification programs, it is important to learn local seed law and certification standards for each state involved in production of a particular source of germplasm. Differences in regulations can mean substantial differences in potential for unintentional selection or crop contamination.

Positive directions. In the last decade, the past emphasis by PMCs to release materials selected and produced for soil conservation purposes has shifted to incorporate more biodiversity-oriented releases, supported by the AOSCA program described in Box 10. The older releases were usually developed under an "agricultural" rather than "ecological" perspective (see Chapter 1). Darris (2003) reports that in Oregon, there has been a shift since 1995 toward providing more source-identified plant releases and other native plant materials more appropriate for restoration (often referred to as ecotypes). The PMC in Corvalis works closely with the Pacific Northwest Region Forest Service, other agencies, and groups on common garden studies designed for evaluating species-specific seed transfer zones such as described in Chapter 6. They also do seed increase of their releases and for special projects with cooperating agencies. This and other PMCs supply seeds to commercial seed growers and private nurseries. The USDA Forest Service Shrub Science Laboratory also researches plant materials development in addition to investigating wildland revegetation techniques. They shifted emphasis to a biodiversity context many years ago and have been leaders in the field (Monsen and Shaw 2001).

Within the Forest Service, the J. Herbert Stone Nursery in Oregon has been developing methods for production of native grasses and forbs since 1992. They have met with much success and are helping to provide important information on growing techniques and production methods to the public while increasing native plant germplasm for agency projects (Colleen Archibald, pers. com.). Some native germplasm is provided to commercial seed growers.

What should you know about available native plant materials?

The genetic uncertainties and ramifications of using wildland-collected plant materials that have no documented source population or collection strategy can differ from those surrounding use of native plant material releases with documented history. The increasing availability of certified plant materials and the increase in natural track classes of germplasm from PMCs is very encouraging. However, proper specification and use of both these newer and the older plant materials is important. The use of certain well-documented materials and older releases can still be a gamble in a biodiversity context. The quality of the seeds and their genetic appropriateness will depend on many factors, some which are noted below. Table 8.2 lists NRCS plant materials releases from Englert et al. (2002) for species that occur in Region 2. The table also provides background information about native plant material releases whose germplasm originated at least partly from within Region 2. This table can be used in combination with Chapters 9-11 and the information in this current chapter to provide an appreciation for the background of many releases. The information should also help guide information gathering for newer releases and other materials available from commercial sources.

In addition, each PMC in Region 2 (and in the west) provides a list of “conservation plant releases” on their website (NRCS-PMC 2004). Table 8.3 shows conservation plant materials released from one of five PMCs serving Region 2. Each PMC in Region 2 has a similar table. On the PMC websites, many releases in the tables have links to release notices, planting guides, and information brochures. For the example in Table 8.3, each species has a link to information. Some sites have detailed information available, for example, site of origin, collection site conditions, year collected, information about germplasm testing, known tolerances, and recommendation about use in wildland habitat (more complete for some releases than others)

1. How was the original germplasm collected and processed (what guidelines)? For all wildland-collected and pre-varietal germplasm, the importance of the initial germplasm collection cannot be overstated, but the appropriateness will vary depending on project context. Here we focus on materials used to restore native biodiversity, incorporating genetic concepts explained in Chapters 4-7, recognizing that some standards could be relaxed for materials used for other purposes. For biodiversity interests, wild germplasm should be collected from natural populations, avoiding areas previously planted with off-site sources or from a small number of samples. Sampling methods should reflect the genetic diversity of the native population and avoid potential for excessive inbreeding. If accessions were mixed for the market, they should have been mixed in a way that avoids potential outbreeding depression. If the populations were mixed before increase, the same issue applies. For wildland restoration, except under exceptional circumstances, there should have been no purposeful selection of phenotypes during collection (Meyer and Monsen 1993, Knapp and Rice 1994). The plant with the smaller shoot, for example, might have the larger, more drought tolerant root system. That is, the collection should have been as random as possible, not selecting for any particular traits. Get answers to as many of the following questions as possible.

- Was sampling from many (versus few) maternal parents or from many (versus few) populations?
- What was the extent of mixing differentiated populations?
- What were the differences between mixed populations?
- Is it likely that genetic diversity was low in the original germplasm collection because it was based on only a few clones or individuals?
- How far apart were sample plants?
- Was there active selection of phenotypes/genotypes?

Germplasm collected for direct seeding, seed increase, or development of cultivars, has not always been collected to reflect genetic diversity of the source population. It is worth checking what is known about the original samples used to develop particular cultivars and to be aware of why the material was produced. There are many competing project goals in plant materials development, some of which may not be complementary to most wildland projects. For example, the germplasm may have been selected and developed to rehabilitate high altitude mine sites, to provide pasture for domesticated animals, or to provide quick plant cover to control erosion. When inserted into natural communities, such materials may perform very differently than local native materials. The size of the collected population, the number of plants sampled, and the distance between samples can have a large impact on genetic diversity of the collection. Population genetic models predict that the smaller the initial sample, the higher the potential for loss of important adaptive variation, random genetic drift, and inbreeding depression (see Nei et al. 1975, Ellstrand and Elam 1993, Montalvo et al. 1997). Work with experimental populations of plants has shown that initial population size and the spatial arrangement of populations influences rates of inbreeding, inbreeding depression, and genetic diversity consistent with expected patterns (Richards et al. 2003).

There are some rules of thumb about how many samples to collect from a population to capture at least 95% of the alleles while devoting the least amount of effort (Falk 1991, Dvorak et al. 1999, Brown and Hardner 2000). It is well known that the number of alleles found in a natural population increases proportionately with the size of the population (on a log scale). This means that more samples are needed to capture variation of larger populations than of small populations. The biology of the species can also have a large influence on the minimum number of samples needed to maintain viable populations. Because inbreeding increases the relatedness of gametes in any local area, the number of samples needs to increase as self-pollination increases. With respect to sampling for seed banks, Brown and Hardner (2000) estimated that about 59 unrelated gametes are required to obtain 95% of the alleles in a local population, but that this number should double if alleles at different loci are represented at equal frequency. This means that at least 30 to 60 random individuals (or clones) should be sampled in a completely outbreeding population (that is, not inbreeding). If there is substantial self-pollination, the minimum sample would be about 60. If the samples are collected from multiple stands or populations (50 or more) to represent the variation in an ecoregion, the minimum number of individual plants to sample per population drops to about 15. Smaller samples will very likely result in genetic erosion. Such models are based on discrete molecular markers and may underestimate the sample sizes required to preserve quantitative trait variation that is tied to fitness. In additon, Falk (1991) points out that when there is a goal to maintain biodiversity, collecting only the minimum to maintain viable populations is risky when our understanding of species biology is incomplete. In addition, the goal is not to reduce populations to their survivable minimum. This argues for collecting more than the minimum sample size prescribed by theoretical models.

For seed increase of native grasses and forbs, many more than 60 individuals will normally be sampled from the natural parent population or groups of local populations. The NPMM (2000) recommends using seeds collected from at least 200 individuals for production of source-identified seed. When seeds are collected and bulked for direct seeding into wildlands, many individuals are often collected. When samples are well-spaced across populations, the higher the number of samples, the higher the probability of capturing a high percentage of the genetic variation in the population.

It is important to note that some releases have been developed from only a few samples, including some natural track releases (for example, Maximilian sunflower, Medicine Creek Germplasm, Table 8.2), and some private seed companies keep sketchy records of sampling strategies.

Note that if a shrub or tree release does not conform to the Region 2 Seed Handbook (germplasm collections and deployment standards) then the material is not appropriate to use in Region 2 National Forests and Grasslands. Check what collection guidelines were used. The Forest Service has been proactive in developing collection rules for woody plant accessions that assure genetic diversity and ample documentation for tracking purposes. Within the past decade, these rules have been modified into guidelines for collection of grasses and forbs. Currently, species that occur in large populations are often wildland-collected in bulk and contain seeds from many individuals. In addition, if accessions of seeds are field increased to multiply seeds before planting in wildlands, the guidelines will assure adequate sample sizes and avoidance of accidental shifts in genetic variation, genetic erosion, and the problems that can arise from inbreeding and loss of adaptive variation. Of course, sampling methods should be modified based on life form, outcrossing potential, and gene dispersal abilities. Proper labeling of accessions and record keeping about collection details are important. Without good records, there is no assurance that purchased plant materials will have been produced from accessions that represent the diversity of the native population.

2. Was collection location and subsequent treatment well documented? It is important to know if the germplasm was collected from natural populations (versus previous revegetation areas), documented, tested for weed content (especially if seeds are to be used for direct seeding), increased in production fields without selection or testing, or selected and bred for some specific purpose. Federal agencies such as the PMCs and USDA Agricultural Research Service (ARS), and Forest Service research labs and nurseries have procedures for documenting seed accessions intended for plant improvement programs or pre-varietal releases. Although inconsistently used in the past, federal agency documentation and tracking procedures are currently very thorough, the rigor of their operations makes official certification unnecessary for seed obtained directly from their planting or seed increase projects. However, when materials must be obtained from the private sector, certified germplasm has a higher probability of being properly labeled and processed than seeds that aren’t certified.

3. How might cultivation, selection, and harvest practices have affected genetic diversity? Many of the same principles used in the production of trees may be applied to agricultural production of other native plants. Tree improvement programs have employed methods to decrease unintended genetic changes during cultivation for a long time (Kitzmiller 1990) and the practices used to produce non-tree plant materials deserve as much scrutiny. Much wild-land collected germplasm of grasses and forbs is field increased, and occasionally shrub species are cultivated for seed production. This makes seeds available in larger quantities than initial smaller collections, often by orders of magnitude. The practice can result in lower costs of seeds and it can protect native populations from over harvest. When germplasm is field increased or purposefully selected for special purposes (as in cultivars or selected classes of native plant germplasm) there are some important genetic precautions to consider before using the materials in wildland situations.

Unintentional selection of traits and genetic erosion: Planting methods, harvest practices, and field location can cause unintentional genetic shifts in traits and the erosion of genetic variation during agricultural production of native plants (Meyer and Monsen 1993; Knapp and Rice 1994). Many native species have important traits that are selected against under cultivation and during harvest. For example, seed dormancy and seed shattering (aids seed dispersal) can be important adaptive traits in plant species, but these two traits are often selected against and lost unintentionally due to standard cultivation and harvest practices (Cai and Morishima 2002). Many species have variation in seed dormancy. If seeds are not pretreated to break dormancy before planting, and the increase crop is grown under conditions that do not break dormancy of most seeds, the trait can be lost after several generations of seed increase. Growth rate and the timing of flowering and fruiting are other traits that are subject to unintentional selection. Harvesting seeds in a narrow time window can squeeze genetic variation for timing of flowering, while harvest toward the end or beginning of seed maturity can result in genetic shifts in the trait. Intentional selection (such as forage quality) can potentially result in unintentional selection of other correlated traits (for example, see Gustafson et al. 1999). Unfortunately, seeds two or more generations down the road are seldom tested for genetic shifts. Many growers keep careful records of planting dates, harvest dates (estimates peak maturation time), and seed germination and viability for each harvest. If the percentage of ungerminated, viable seed (hard seed) increases significantly after each harvest, there may have been a genetic shift. However, seed dormancy can be influenced by both genetics and the environment experienced by the maturing seed, clouding interpretation (Meyer and Monsen 1993). Regardless, growers can often provide information about seed tests and crop maturation time useful to detecting shifts.

To minimize unintentional selection, the NRCS—in an agreement with certifying agencies—allows a maximum of four generations of seed increase for cultivars, tested releases, and selected releases. For some species, fewer than four generations are allowed (NPMM 2000). Private companies do not have to follow the same rules as the PMCs. Both the NRCS and AOSCA provide standards for the private seed industry and allow unlimited generations of seed increase for source-identified seeds. This assumes no genetic shifts or erosion—but this assumption needs to be carefully examined. Each state may further restrict the number of generations according to state seed law. Seed providers must follow local seed laws and AOSCA standards for seed certification purposes, but it is good practice to check that attention has been paid to the possibility of unintentional selection.

It is also important to know how well isolated a particular crop was relative to other populations with which it could cross-pollinate. Standards for distances between fields, known as isolation distances, vary. If the production field is not certified, there is no guarantee that isolation distances were acknowledged. AOSCA certification programs may set different standards in different states, and standards may be modified for different species if data support doing so. For example, in California, source-identified crops were initially classified into “selfed” versus “outcrossed” and required at least 15 feet between fields of the same selfing species, and at least 165 ft between fields of an outcrossing species. This dichotomy was modified after it was realized that some “selfing” species also cross-pollinated (A. Montalvo, personal observation; served as a cooperator and source-site inspector for California Crop Improvement Association’s Wildland-Collected program). As explained in Chapter 5, many species have mixed mating systems, and species that frequently self are known to sometimes outcross (reviewed by Waines and Hedge 2003). Attention should also be paid to variation in pollen dispersal distances for animal pollinated plants.

Intentional selection or breeding process? The development of cultivars from native plant species can result in releases that are quite different from natural populations. Mayer and Kitchen (1995) pointed out that the point of plant breeding is often to produce uniform races to be utilized under particular circumstances. The National Plant Materials Manual lists 18 distinct categories of plant improvement projects (NPMM 2000). These include plants for croplands, forest-lands, mined areas, pasture, natural areas, wildlife, water quality, and urban areas. For example, a number of cultivars have been selected based on some aspect of forage quality for domesticated animals such as ruminant digestiblity (Vogel and Pederson 1993, Redfearn et al. 1999). Some plant materials have been purposefully selected under the genetically manipulated track (Figure 8.1) for seed retention or lack of seed dormancy to make seed production more efficient. For example, Ribstone Indian ricegrass (*Achnatherum hymenoides*) was released as manipulated track, selected class germplasm. It was selected from few individuals for seed retention (Jones et al. 2004). Many other native plant materials have been chosen and selected for erosion control, pasture, or purposes apart from restoration of wildlands. Many releases, especially the older ones, also have a narrow genetic base (but see Gustafson et al. 2004b below). Such selection criteria are not necessarily compatible with long-term population viability or diverse community interactions. It is important to know how and why a cultivar was bred because some selected functions may be fully appropriate for particular types of revegetation projects while being inappropriate for others, especially wildland restoration.

Studies of genetic diversity, genetic shifts, and performance in cultivars. Some cultivars have been selected from very few individuals and have been cultivated for many generations. Examples of releases developed from fewer than six individuals from Table 8.2 include *Elymus canadensis* 'Mandan', *Amelanchier alnifolia* Newport germplasm, and *A. alnifolia* Okanogan germplasm. Genetic erosion, inbreeding, and the consequences for long-term success of wildland populations have been taken seriously by breeders of native plant materials in recent years. The concern resulted in a number of studies with molecular markers that compared the genetic diversity within and among accessions of wildland-collected seeds and various kinds of plant material releases, including some cultivars. Studies of neutral marker variation (Chapter 5) are a quick way of determining if there has been an overall loss of genetic variation. Comparisons of molecular marker variation of a source population and germplasm derived from the population can detect genetic erosion in the germplasm. A random loss of neutral alleles may coincide with a loss of alleles that control adaptive traits. However, marker studies cannot detect changes in adaptive traits, such as shifts in cold hardiness or percentage of dormant seeds. Likewise, shifts in adaptive traits caused by natural or artificial selection are not expected to affect the distribution of variation in neutral markers (unless marker variation is itself adaptive or linked to an adaptive trait).

Phan and Smith (2003) used DNA techniques (RAPDs) to detect a possible genetic shift among source populations and the derived cultivars of blue grama (*Bouteloua gracilis*), a highly outcrossing perennial grass with a wide distribution. Samples from 11 natural source populations were grown in a field nursery and contrasted with two selected composite populations created from the planted populations. One of the selected populations (BMSC) was a composite of 99 clones from the 11 source populations selected for seed yield while the other was a mass-selected composite of 25 clones (MSC). Over 97 percent of the variation was detected within natural populations. Highly significant changes in RAPD patterns (molecular marker) were detected between the natural and selected populations, but the estimated genetic shifts were only 0.6%-1.9% (source populations relative to BMSC and MSC, respectively). Further analysis of AFLP variation revealed significant genetic differences among several germplasm populations (BMSC, the ecotypes Bad River and Minnesota, and a native seed collection from Manitoba; Fu et al. 2004). The composite BMSC was the most variable as expected. But they found no evidence of genetic erosion in BMSC after two cycles of seed increase. These studies indicate that genetic erosion resulting from active selection was small in the short term.

Gustafson et al. (1999) examined samples of cultivars and native populations with DNA markers (RAPDs) from six remnant Grand Prairie populations, two Illinois prairie populations, and two cultivars of big bluestem (*Andropogon gerardii*). Genetic diversity was high and mostly due to within population variation. There was a significant negative relationship between genetic similarity and geographical distance, consistent with isolation by distance. Small, isolated remnant big bluestem populations did not have significantly lower genetic variation than the other populations studied. In a later study, Gustafson et al. (2004b) examined genetic diversity of big bluestem and indiangrass (*Sorghastrum nutans*) from seven remnant and six restored local tall grass prairies and non-local remnant prairie. The restored sites were established with seed from a mixture of at least two local populations. They also included three cultivars of big bluestem (‘Roundtree’ [Rountree], ‘Pawnee’, and ‘Kaw’) and two of indiangrass (‘Rumsey’ and ‘Cheyenne’). DNA marker analysis (RAPD) showed genetic diversity did not differ among restored or remnant populations or cultivars. The restored populations and cultivars were as genetically diverse as remnant populations. However, local, remnant, and restored populations were genetically different from the non-local remnant grasslands and were consistently different to the cultivars. This research indicates that genetic diversity may be less of an issue in these perennial outcrossing autopolyploid grasses than genetic differences among local, non-local, or cultivar seed sources. They predict that translocating non-local seed to increase diversity, or using cultivars, is likely to alter the genetic structure of remnant populations and potentially influence the associated community and ecosystems.

Larson et al. (2000) examined genetic diversity in bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Löve) cultivars compared to the second generation of a new composite line called ‘P-7’. They found that P-7 had higher genetic variation and fewer monomorphic loci than the cultivars derived from single populations (‘Goldar’ and ‘Whitmar’), but that the two cultivars did not appear to have undergone much genetic erosion, possibly because the species is highly outcrossing. Given the interesting details of its development (see below), it is no surprise that P-7 is more genetically diverse than these other cultivars. As indicated in previous chapters, genetic diversity is only one of the important factors in determining if a plant material is appropriate for a particular site. The extra diversity produced from hybridization can be a double-edged sword. Sometimes it will be beneficial and sometimes detrimental.

Increased genetic variation using multiple population crosses. The perceived risk of genetic erosion has resulted in a shift away from narrowing the genetic base of cultivars and other releases toward optimizing genetic variation and minimizing genetic erosion. This is sometimes done by mixing many populations together during plant materials development. For example, Burton and Burton (2002) mixed seed accessions from many populations in the same production field to maximize hybridization and possible heterozygosity in seeds offered for restoration (11 native grass, four graminoid, and 16 forb species). Their particular example combined seeds from a single region of British Columbia. However, plant breeders sometimes do composites and polycrosses of many populations from many different areas, sometimes from contrasting ecoregions, subspecific taxa, and ploidy levels in development of cultivars.

For example, bluebunch wheatgrass ‘P-7’ mentioned above is a multiple-origin polycross of 25 diverse populations, mostly diploid, a tetraploid population, and two diploid cultivars, ‘Whitmar’ and ‘Goldar’ belonging to different subspecies (Table 8.2). There is also a large range of quantitative variation in the species. For example, Kitchen and Monsen (1994) tested 'Goldar' and 47 accessions from natural populations in 9 geographic regions. They found significant differences in seed weight and germination rate at $15/25^{o}$ C (night/day temperature) and at 1^{o} C, Some of these differences could have been environmentally induced. However, the differences in germination response to different temperatures were so large, that some genetic differences in the populations are likely. There were also big differences in emergence, and dry weight. The effect of P-7 or native populations of the same species has not been tested. The species is an outcrosser (Chapter 10, Table 10.1) so potential for hybridization among populations is large when flowering overlaps with that of resident populations. Inbreeding depression within these genetically diverse polycrosses is unlikely to be a problem, but there is a potential for outbreeding depression when they hybridize with native populations. There is variation in cytotype (diploids and tetraploids) and therefore a potential for lowered fertility of crosses between cytotypes.

The resulting diversity of cultivars and other release types is represented by a continuum from genetically narrow selected materials, to genetically diverse pre-varietal germplasm (including natural track such as source-identified), to very genetically diverse composite lines. But the continuum is more three dimensional than linear. One axis may include no selection (only random loss of alleles), another axis may refer to selection for a particular trait (reduced variation), and the third axis may be selection for broad tolerances. The highest genetic variation does not necessarily equate with high adaptation to a particular site.

4. Were releases evaluated for environmental impacts and risks to native populations? In the last century, there was no formal environmental evaluation of conservation releases. Starting with the new millennium, the USDA NRCS Native Plant Materials Program began requiring completion of an environmental evaluation of each plant material it wishes to release. A nine-page exhibit is devoted to evaluation of potential adverse environmental effects (NPMM 2000, Exhibit 540-31). A scoring system helps quantify effects. The evaluation covers aspects of population persistence, aggressiveness, and ease of control recognizing that some releases may be invasive. Questions cover: 1) ability to invade natural systems where the species does not naturally occur; 2) potential negative impacts on ecosystem processes; 3) impacts on composition of plant communities; 4) allelopathic effects; 5) impact on habitat for wildlife or domestic animals, including threatened and endangered species; and 6) impact on other land use. The evaluation also covers ease of management, conservation need, and biological characteristics such as reproductive mode, age to first reproduction, seed bank persistence, and other factors that influence reproductive success and persistence. Finally, the evaluation asks if the cultivar hybridizes with other species.

This new risk evaluation framework represents a great improvement to the ability of land managers to estimate the potential effects of newer releases. Application of the framework to older releases could also prove beneficial. Nevertheless, the evaluation framework for risk analysis could be strengthened with some added questions and by considering that lack of information for a particular evaluation category can actually be risky. Although few of the risks noted in the questions have been evaluated experimentally for many materials, the evaluation framework does not currently provide a response for “effects unknown”.The official evaluation also does not address the potential for adverse effects of outcrossing to resident populations, or if there may be adverse effects from introgression and genetic swamping of wild populations of the same species. For materials planned for restoration of wildlands or revegetation projects next to wildlands, it would be helpful if these additional risks were evaluated and made available. Some risk factors that have had little attention are described below.

Differences in diversity and function compared to resident native population*:* Many species chosen for development and release are common and widely distributed in nature, and show large morphological and genetic differentiation among populations from different habitats or regions. Cultivars may vary considerably in how similar they are to native, wild populations of the same species, especially if they have been selected from few individuals or derived from mixing populations collected from distant areas or different ecological regions. Highly selected or mixed cultivars are not well suited to areas with the goal of maintaining natural levels and types of diversity. Neither promotes natural biodiversity. Highly selected cultivars can result in genetic erosion and homogenization of species populations. They can also interact very differently with other plants and animals due to differences in growth patterns, chemistry or other attributes. Although mixed cultivars with artificially high levels of diversity may decrease inbreeding depression, they also increase the potential for outbreeding depression. Neither situation is optimal. However, highly selected, or diverse composite mixtures may be useful for reclamation of highly damaged sites or a rehabilitation or restoration goal that doesn't include preservation of native biodiversity (such as restoration of pastureland for livestock). Some selected germplasm or cultivars may also be useful in severe situations where invasive species have displaced native communities through competition and altered fire cycles. However, natural species populations may be perfectly suitable for this purpose (Brown and Amacher 1999). In general, for wildland revegetation with a natural biodiversity goal, non-local germplasm or manipulated cultivars may be less suitable than natural track plant materials derived from regionally local populations (see natural track pre-variety germplasm in Figure 8.1). In addition, cultivars may also not be the most economical or effective choice in revegetation. If pre-varietal releases of local germplasm are made available, they may be more beneficial and cost effective in the long term because of lower risk of inappropriate adaptation, ploidy levels, genetic diversity, and community interactions.

For any restoration project, the historical condition identified as the restoration goal will affect the choice of plant materials (Monsen and Shaw 2001). If the goal is to assist a trajectory toward a historical, native condition, including interactions among species, then local plant materials may be the most logical choice. There is insufficient data to support the common assumption that non-local or manipulated native plant material will function in the same way within the ecosystem as resident genotypes. Rather, there is data to the contrary (Jones and Hayes 2000; Humphry and Schupp 2002; Gustafson et al. 2004a). Research that tests if genetic and ecosystem integrity will be upheld using translocated plant materials is seldom done. Most research on released plant materials examines how the translocated population performs relative to other populations of the same species, usually in isolation of other species. That is, assessing the effect of hybridization or community interactions is very rarely examined.

The classification of plant materials helps in recognizing degrees of potential differences between a particular plant material and the populations native to a site. As was explained in Chapters 5-7, it is not just similarity in local adaptation that affects the success of populations, but other aspects of genetic similarity such as chromosome number, structure, and differences in co-adaptation also play a role.

Evolution or emergence of new invasive genotypes. Some of the hypotheses about the causes of the evolution or emergence of invasiveness are relevant to native species. For example, large latitudinal range can be a good predictor of potential invasiveness (Rejmánek 1995). This is consistent with the idea that many invasive species have "general purpose genotypes" that have broad environmental tolerance and high levels of phenotypic plasticity (Baker 1995). Polyploid members of species having a series of diploids and polyploids have also been implicated as having a greater chance of colonizing new sites, naturalizing, and becoming invasive (Stebbins 1965). Such correlates of invasiveness are typically weak and there is also an element of chance (Ellstrand and Shierenbeck 2000). For example, when genetically differentiated populations are moved around by humans, the shifts in floristic composition, genotype compositions, and species interactions can result in variation in competitive hierarchies and invasiveness (Rice 1998). The planting of cultivars that were selected for aggressive growth into a diversity of wild sites may provide similar shifts in competitive hierarchies of interacting species.

Ellstrand and Schierenbeck (2000) noted that some of the European and Eurasian annual grasses introduced to the western US may have emerged or evolved into aggressive populations following multiple introductions from diverse sources. In these situations, there is also the potential for hybridization with resident populations of the same species. With repeated hybridization opportunities, even if there is outbreeding depression, there may be some rare, new genetic combinations that do very well if in the right place. New genetic combinations can be tested in multiple new environments, possibly leading to the formation of new invasive genotypes. Published studies of new invasive genotypes forming from hybridization of local native genotypes with cultivars bred for conservation purposes are lacking. However, worldwide, there is ample evidence for hybridization of highly selected crop plants with wild populations of related species (Ellstrand 2003, Hedge and Waines 2004). Some of these have become important agricultural weeds in the US and elsewhere. It is not far-fetched that highly selected cultivars will sometimes hybridize with resident, native individuals to produce some offspring with aggressive tendencies.

With or without hybridization, numerous species introduced to areas outside their historical ranges and into areas with similar climates have become aggressive invasive species. Similarly, some introduced genotypes of native species may be capable of competitively swamping resident populations causing cryptic invasions (Hufford and Mazer 2003). Such swamping can be greatly aided by intentional translocations and by clonal growth. At least two clonal species have become invasive after introductions of germplasm to different continents *within* the species range. These cryptic invasions of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) and reed canarygrass (*Phalaris arundinacea* L.) have become a serious problem in many wetland areas in the US. In addition, some native plant materials used in the wrong habitats outside their native ranges can become serious and aggressive competitors—especially if they are selected or bred to be aggressive (Box 6).

The case of common reed has the best documentation (Chambers et al. 1999, Saltonstall 2002). The historical distribution of genotypes seen from herbarium collections has changed drastically in the past 150 years. North American genotypes were once limited in distribution, less aggressive, and very different genetically from Eurasian populations. Current phylogeographic and range data suggest a rapid expansion of populations introduced to seaports, aided by extensive clonal growth. The introduced genotypes swamped the native populations of New England and then invaded interior freshwater wetlands throughout North America. There has been a homogenization of genetic variation and a reduction of population structuring. Note that reed canarygrass is largely clonal and plants tend to produce apomictic seeds and spread vegetatively. Hybridization between Eurasian and North American clones has not been documented. The invasiveness might be due entirely to higher competitive and colonizing capabilities of introduced material. Such documentation for reed canarygrass has not been provided (see Morrison and Molofsky 1999).

Broad adaptation and competitive effects of cultivars or selected releases. The testing and selection programs for natural track native plant releases embrace the conservation of local adaptation. In contrast, the programs for manipulated track releases frequently discourage or eliminate local adaptation, and encourage broad tolerances so that the seeds will do well in a variety of habitat conditions, the “jack of all trades” or “general purpose genotype.” Some have asked if use of broadly adapted cultivars increases the risk of hidden tradeoffs in survival or reproductive potential or to new invasive potential. For example, a recent study with native grass cultivars by Gustafson et al. (2004a) examined populations of big bluestem (*Andropogon gerardii*) in a series of competition experiments. They detected differences among native provenances, cultivars (‘Rountree’ and 'Pawnee'), and non-local provenances. Cultivars were consistently larger in greenhouse studies than local and non-local plants regardless of competitor density and identity. Furthermore, in field plantings non-local plants were significantly smaller than both local provenances and cultivars. The study showed that provenance and history of the plant material (selected versus natural germplasm) significantly influenced competitive ability and that there were differences in adaptation among test populations. The higher competitive ability of the cultivars suggests they can out compete and potentially swamp local genetic resources in this outcrossing species. Such competitiveness may be fine for a pasture situation, but can be deleterious to a natural ecosystem. It may be difficult to overcome the tendency to develop highly competitive plant materials in a breeding program where the most vigorous individuals or accessions are often selected for production of the next generation rather than random samples.

Some other agricultural production practices, such as mixing of many populations together from widely ranging geographical populations, may increase the chance that a release has at least some genotypes adapted to a particular planting situation. The same practice also increases the chance of outbreeding depression or that some genotypes will become aggressive, invasive, or interact differently with other species. There may be significant genetic differences in growth patterns, palatability, competitive interactions, or other traits compared to the local native population. It is important to consider the risk of changing interactions with other organisms for any project that has biodiversity interests at stake. Recent research trends may provide data useful for weighing the benefit of luxuriant growth of some releases, against the risk of undesired cascading effects through ecosystems. Risk levels will differ among species, plant materials under consideration, and planting sites.

To avoid unforeseen consequences of using non-local selected, tested, or cultivar germplasm, it may be prudent to consider more than which release is the most robust grower or which release is the most genetically diverse. Consider what is compatible with native populations and what is *sufficient* cover to do the job of soil stabilization and jumpstarting the restoration process. Sometime the best material in terms of survival and biomass can be detrimental for regeneration of natural plant communities and biodiversity. The agricultural line that performs best over the broadest range of conditions might be too aggressive or competitive to allow desired establishment of a whole host of genotypes and species. On the other hand, aggressive cultivars may sometimes deserve a staring role in restoring (or rehabilitating) habitat that has been invaded by aggressive exotic species and otherwise cannot be successfully returned to a native plant community. Invasive or very aggressive species can significantly alter success of other species or genotypes and alter restoration potential. Their use should be carefully considered with respect to project goals. Some of these possible environmental consequences are evaluated in the current decision tree for deciding on release of plant materials from PMCs (NPMM 2000, Exhibit 540-31).

If considered as a nurse crop, does a particular non-local release have attributes to prevent gene flow into native population or aggressive takeover? Native biodiversity must be part of the goal of revegetation projects within federal wildland areas. As has been explained in previous chapters, inappropriate decisions can have irreversible effects on biodiversity. It is important, as pointed out in Chapter 3, and Box 5 *To Seed or Not to Seed*, to evaluate whether or not temporary revegetation is actually necessary or beneficial. Often, natural regeneration is adequate. Sometimes, if no appropriate plant materials are available and it is determined that temporary plant cover or a nurse crop is necessary, there may be exploration of non-local plant materials or non-persistent, non-native species to fill the void. It is important to make informed, science-based decisions and choose appropriate plant materials to meet the project objectives. The information noted under questions 3 and 4, together with 6-7, will be very important to consider when deciding on the appropriateness of the particular material. Lesica and Allendorf (1999) discuss the use of plants that do not outcross and that have little ability to persist. They also suggest that cultivars are appropriate only on small-sized (and very severe) disturbances in order to limit geographic distribution and potential adverse impacts. It may be useful to consider using such materials if they have no ability to spread vegetatively and will not produce seeds in the habitat where the nurse crop is needed. A number of tested, selected, and cultivar releases are known to fail to flower when moved too far north, south, or among elevations (see example of ‘Garnet’ mountain brome and other severe mismatches in Chapter 7). If such plantings die off within a season or two, they could be of value for temporary cover—but if the right climatic circumstances occur for them to sexually reproduce, then maladapted genes could spread into the wild population. Perhaps there should be buffers of some kind to prevent gene flow into resident populations.

5. Are there potential cumulative impacts from repeated extensive use of a limited number of cultivars? There has been no evaluation of how widespread and continued use of manipulated track cultivars, especially those that were low in genetic diversity, has affected native populations. Some early cultivars are still in use after more than 50 years, and they have been repeatedly introduced to large geographic areas in the western U.S. The potential harmful effects to communities and genetic resources resulting from the spread of cultivars across large areas over a long period of time is potentially significant if the cultivar populations persist and either breed with native populations or compete with them for limited resources. Limited resources can include pollinator or seed dispersal service, sunlight, nutrients and so on. A related issue is that extensive cultivar usage can impede future efforts to develop local native seed sources if one can’t differentiate between introduced material and indigenous sources. When commercial sources are used, it is important to document and map the seeding locations so these areas can be avoided during seed harvesting activities. In some areas, it can be difficult to determine if the stand of plants was seeded previously or is natural.

Summary and action plans for obtaining information on plant materials

Ideally, plant materials for revegetation of National Forests and Grasslands will be collected from native plant populations under Forest Service direction. When necessary, the collections would then be increased in production fields without any genetic manipulation—as in the natural track in Figure 8.1—and by using cultivation and harvesting techniques that minimize unintentional selection. When planting is necessary after large, unplanned disturbances such as wildfires, such seed supplies may be in short supply. When seeds are considered for purchase to augment natural regeneration or local collections, it is important to know as much as possible about how the seeds were collected, tracked from collection to distribution, and increased. Only then can informed choices be made.

Available information on specific plant materials varies considerably. For wildland revegetation projects with a biodiversity context, it is wise to avoid plant materials that have uncertain information about their origin or cultivation history. It may also be prudent to avoid plant materials that are very different from local native populations or that have been genetically manipulated and bred in ways that will have unknown effects on existing native populations, communities, and ecosystems. Table 8.4 provides a summary of procedures that could be useful in retaining genetic diversity of collections and reducing unintentional selection during cultivation. Table 8.5 summarizes the questions covered in this chapter and provides examples of responses and comments about possible genetic effects. It would be possible to expand this table to include columns that accommodate additional site situations and project goals—for example, if the goal is revegetation of toxic areas degraded by mining.

Obtaining information on plant materials releases and marketed seeds is often at your fingertips through websites and publications. This allows one to see if plant materials available are of unknown origin or of documented origin. If documented, there is often information that hints at whether or not the particular plant materials are likely to be genetically appropriate for a particular wildland site for which native biodiversity is an important goal. Table 8.2 summarizes information on the most prominent cultivars and other plant materials releases of some species native to Region 2. Additional information can be found at each PMC website.

Changing societal values and needs have resulted in a dramatic increase in diversity and commercial availability of native plant materials (McArthur and Young 1999, Monsen and Shaw 2001). Similarly, societal needs could encourage commercial seed producers to provide details about the seeds they develop and market. Such information would remove much uncertainty about commercial plant materials and make those seeds more attractive for purchase and use on public wildlands.

Table 8.1. Specifications for the different classes of native plant germplasm made available for release by USDA Plant Materials Centers. Table is adapted from the Native Plant Materials Manual (NPMM 2000, Exhibit 540-33). The criterion for ecological impacts (for example, evaluation of invasiveness) was added in 2000. Protocols have not been established for assessing the possible deleterious effects of hybridization among source populations. All except the germplasm class are eligible for certification. This table applies to both natural and manipulated track germplasm for those classes that can be manipulated (see Figure 8.1).

	Release type				
	Source-identified	**Selected**	**Tested**	**Germplasm**	**Cultivar**
Selection basis	No human selection of material	Based on initial data, population is superior to others in some way that will meet client needs	Material has proven genetic superiority/ distinctiveness	Material has trait/s that may be of value for further plant breeding	Material has proven genetic superiority/ distinctiveness
Criteria for release	Species literature search to be conducted	Species literature search to be conducted	Species literature search to be conducted	Species literature search to be conducted	Species literature search to be conducted
	Original site (soil, climate, other physical and geographic factors) and plant population data	Original site and plant population data	Original site and plant population data	Original site and plant population data	Original site and plant population data
	No evaluation data	data on a site representative of conservation need	advanced evaluation data replicated at multiple sites	advanced evaluation data replicated at multiple sites	advanced evaluation data replicated at multiple sites, field plantings
	Not applicable	Multiple years of data (1-4)	Multiple years of data (3-6+)	Multiple years of data (6+)	Multiple years of data (6-9+)
	Plant does not post threat through invasiveness or poisonous substance	Plant does not post threat through invasiveness or poisonous substance	Plant does not post threat through invasiveness or poisonous substance	Plant does not post threat through invasiveness or poisonous substance	Plant does not post threat through invasiveness or poisonous substance
	No comparison to other accessions required	Compared to other accessions/cultivars	Compared to other accessions/cultivars	Variable	Compared to other accessions/cultivars
Limitations of generations	Unlimited generations allowed; all germplasm types collected from natural stands are designated G0	If field grown, generations limited to maximum of four; if wild collected, unlimited generations allowed.	If field grown, generations limited to maximum of four; if wild collected, unlimited generations allowed.	Not specified	If field grown, generations limited to maximum of four; if wild collected, unlimited generations allowed.

Table 8.2. Information about releases of plants native to Region 2. Taxonomy follows USDA, NRCS (2004). If there were many releases for a particular species, only those derived from collections within Region 2 are listed. A number of species are also in Chapter 10 (Tables 10.1-10.5). Those tables can be consulted for species traits and genetic studies. Englert et al. (2002) lists releases from PMCs and cooperators through September 2001. Alderson and Sharp (1993) provides some detailed information about native grass cultivars developed or under development by PMCs and the ARS. Additional comments are from individual papers, from Ogle et al. (2003), and from release notices available through PMC web sites. Further information can be obtained directly from the PMC or ARS lab that developed the release. Information on sample sizes of original collections is provided only if in release notice or publications. Note that environmental evaluations prior to release of new PMC plant materials were not required until 2000. Information from release notes posted on PMC web site are cited as “release notes.”

Species	**Common name**	**Englert et al. 2002 (release type, where collected, year released)**	**Alderson and Sharp 1993 (notes about releases)**	**Additional comments**
Grasses:				
Achnatherum hymenoides (Roemer & J.A. Schultes) Barkworth (=*Oryzopsis hymenoides* (Roemer & J.A. Schultes) Ricker ex Piper; *Stipa hymenoides* Roemer & J.A. Schultes)	Indian ricegrass	'Nezpar' (cult., ID, 1978); 'Paloma' (cult., Pueblo CO, 1996); 'Rimrock' (cult, Yellowstone Co. MT, 1996)	Lists 4 cultivars, 3 involve CO. 'Paloma', coll. In 1957 from near Pueblo, CO at 1,530 m, ~25-30 cm precipitation, bulk increase, tested. CSU-3, selected from Paloma from seed with no dormancy. CSU-10, composite of 10 parent plants (2 from Warner farm, 1 from Paloma, 3 from NM, others from ND and unnamed location).	Some cultivars selected for low seed dormancy and seed shatter (Ogle et al. 2003). Ribstone germplasm selected for seed retention (Jones et al. 2004). Seed dormancy and seed dispersal through seed shatter are likely adaptive in natural populations. 'Paloma' self-compatible, with both chasmogamous and cleistogamous flowers; cleistogamy varies with environment (Jones & Nielson 1989). Outcrossing also evident. Open flowers disperse pollen and plants hybridize with several species of *Stipa* (Johnson and Rogler 1943, Johnson 1963, Jones 1990). Outcrossing rate likely variable.
Andropogon gerardii Vitman	big bluestem	Lists 7 cult., 6 source-id releases. In R2: 'Bonilla' (cult., Bonilla, SD, 1987); 'Kaw' (cult., Riley Co., KS, 1950); 'Sunnyview' (cult., Union Co., SD, 1998)	Lists 8 cultivars, including 4 from R2: 'Bonilla' selected from bulked seed from 2 native stands near Bonilla, SD.; 'Champ' (Reg. No. 2) (clones selected from 5 north-central NE sandhill areas reciprocally crossed with 2 clones from IA introductions and 3 from Pawnee CO., NE; 'Kaw' is a composite of lines selected after at least 4 generations of progeny from 200 accessions collected in 1935 from Flint Hills grasslands south of Manhattan, KS.; 'Pawnee', collected in 1938 from Pawnee C0, NE. Clones of 4 types selected in 1948, polycrossed. Tested 1950-1951, 1953-54 for range and pasture.	Note: 'Bison' from ND (originally coll. Oliver Co., ND) has very early start off lowering relative to other cultivars (20-48 days earlier) (Alderson and Sharp 1993). This suggests there may be important, adaptive variation in this species for maturation time and flowering times to consider, especially if moving up or down in elevation or latitude.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Bouteloua curtipendula (Michx.) Torr.	Sideoats grama	'Butte' (cult., Holt & Platte Cos., NE, 1958); Central Iowa Germ (source-id, Black Hawk Co., IA, 1995); 'El Reno' (cult., Canadian Co., OK, 1944); 'Haskell' (cult., Haskell Co., TX, 1983); Killdeer (Informal, ND, 1963); Northern Iowa Germ., (source-id, comp. from n. IA, 1995); Southern Iowa Germp., (source-id, comp. from s. IA, 1995)	'Butte' (Holt and Platte Cos. NE accessions had superior seedling vigor and establishment than other sources. Collections combined and tested as Nebraska 37, 1948 tests, released in 1958); 'El Reno' (coll near El Reno, OK in 1934; compared with other sources at Manhattan; released in 1944	Kildeer was selected at Bismarck, ND from a composite of collections from native range sites near Bowman and Killdeer, ND where average precipitation is 15 inches (release notes, Bismark PMC). Year of collection not provided.
Bouteloua gracilis (Willd. Ex Kunth) Lag. Ex Griffiths	blue grama	'Alma' (cult., composite,1992 ARS); Bad River Ecotype (sel., Haakon Co., SD, 1996); 'Hachita' (cult., Hachita Mountain, NM, 1980); 'Lovington' (cult., Lea Co., NM, 1963)	'Alma', developed from 270 plants from each of: Hachita (from NM), 'Lovington' (from NM), and PMK-1483 (coll. location not noted). 9055923, derived from plants collected at eight sites east of Front Range from Cheyenne, WY to Maxwell, NM, and Sterling CO to Rok Ford CO; two cycles of recurrent selection; meant for rangeland improvement and parks, lawns.	Bad River Ecotype is natural track, selected class with good adventitious roots (Bismark PMC). Genetic diversity of BMSC (pre-cultivar composite from selection of 99 clones from 495 plants collected from 11 sites across Manitoba), Bad River ecotype, Minnesota ecotype, and a third generation harvest of BMSC were examined for AFLP variation and compared to detect genetic shifts. As should be expected, BMSC had highest genetic diversity among the samples. There was a non-significant decrease in genetic variation after 2 cycles of seed increase of BMSC. BMSC was also shown to have shifted genetically relative to the 11 source populations from which it was derived (Phan et al. 2003).
Bromus carinatus Hook. & Arn.	California brome (for mountain brome, see *B. marginatus*)	'Cucamonga' (cult., Cucamonga, CA, 1949)	''Cucamonga' developed from collection near Cucamonga, CA in 1939. Intended as cover crop, revegetation of disturbed areas, and for post-fire seeding. Annual life-history. 'Deborah' is a cultivar bred from a collection from England and a collection from the Andes intended for hay pasture.	*B. carinatus* and *B. marginatus* are sometimes lumped into single species. *B. carinatus* can be highly selfing. Plants produce mixture of cleistogamous and chasmogamous flowers. Proportionately changes with environment (Harlan 1945).

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Bromus marginatus Nees ex Steud.	mountain brome	'Bromar' (cult., Whitman Co., WA, 1946); Garnet Germp. (tested, Powell Co., MT, 2000)	'Bromar' from source collected in 1933. Mass selected for smut resistance. Rapid growing perennial. Taller and earlier than other releases.	For 'Bromar' map see Native Seed Network (2004). Vigorus, possibly overly aggressive growth in OR test plots compared to natural accession of germplasm (V. Erickson 2004 pers. com.). Can be too aggressive for mixed restoration plantings. At High elevation in CO, does not flower. Short-lived perennial, not good for long-term restoration. Garnet germplasm is a natural track, tested release originally collected from near Garnet, MT. Based on potential for mixed mating, an isolation distance of 900 ft was recommended in release notes (Bridger PMC).
Buchloe dactyloides (Nutt.) Engelm.	buffalograss	Bismarck Ecotype (sel., central ND, 1996); 'Texoka' (cult., composite of KS, OK, TX, 1974)	none	Bismark Ecotype buffalograss is natural track, selected class germplasm adapted for use in the Northern Great Plains (release notes, Bismarck PMC). It is a composite of two vegetative accessions collected in ND in 1986, evaluated at Mandan, ND. This ecotype is composed predominantly of male plants and requires vegetative propagation. *It is appropriate for reduced maintenance plantings and xeric landscaping.* 'Texoka' is a derived from ten selected clones, four female and six male, originally collected from three states before 1960. It has high seed production from a bias in female clone production. Texoka is hexaploid (Budak et al. 2004). Other cultivars are listed in Budak et al. (2004).

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Deschampsia caespitosa (L.) Beauv.	Tufted hairgrass	'Peru Creek' (cult., Summit Co., CO, 1994)	EPC-1460, coll at Peru Cr. Near Dillon, CO in alpine-subalpine meadow at 3120 m elev.; mass selected and tested at several sites, acid tolerant, meant for reclamation and revegetation of high elevation sites, roadsides, and wetland meadows.	In AK, (Helm 1995) 'Nortran' (bred from Iceland and AK collections for revegetation and turf (Anderson and Sharp 1993)) was evaluated with other cultivars in mixtures and alone with respect to influence on establishment of rooted cuttings of Salicaceae species and colonization by native species. Growth of Nortran was aggressive, highly competitive, and severely reduced native diversity. Cuttings of Salicaceae were also smaller in plots seeded with Nortran (and other cultivars). This suggests environmental assessment of 'Peru Creek' and EPC-1460 is needed if use where biological diversity is a goal.
Elymus canadensis L.	Canada wild rye	Lavaca Germ. (sel., Lavaca Co., TX, 2000); Mandan (cult., Morton Co., ND, 1946); Northern Iowa Germ. (source-id, composite from northern IA, 1995); Southern Iowa Germ. (source-id, comp. from s. IA, 1995)	'Mandan' selected by ARS, at Mandan ND from seeds collected near Mandan in 1935. Mass selection from families of two single plants for leafiness, fine leaves, short stature, and rust resistance.	No releases from R2. *Closest release, 'Mandan', too highly selected and genetically narrow for restoration.*
Elymus elymoides (Raf.) Swezey ssp. *elymoides* (=S*itanion hystrix* (Nutt.) J.G. Sm.); three other subsp: 2) *E. e.* ssp. *hordeoides* (Suksdorf) Barkworth 3) *E. e.* ssp. *brevifolius* (J.G. Sm.) Barkworth, comb. nov. ined. 4) *E. e.* ssp. *californicus* (J.G. Sm.) Barkworth, comb. nov. ined.	bottlebrush squirreltail	Sand hollow (sel., Gem Co. ID, 1996); Tusas Germ (sel., comp. from NM, 2001)	9040187, coll near Pueblo, Pueblo Co., CO; 9040189, coll. Near Buford, Rio Blanco Co., CO; both selected from dryland row tested in Upper Colorado Environmental Plant Center; intended for oil shale and coal reclamation and cropland/rangeland erosion control.	Tusas germplasm is recommended for preliminary revegetation of areas dominated by exotic annual grasses and high fire frequency (release notes, Los Lunas PMC). Seeds collected in 1983 from 131 native stands through NM. Six of these (from about 6000 to 7,500 ft elev and two Major Land Resource Areas (MLRAs) were selected based on vigor, late flowering, and seed yield for the composite germplasm. This germplasm was evaluated as non-invasive.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Elymus glaucus Buckl. ssp. *glaucus*	blue wildrye (named varieties and subspecies exist)	'Arlington' (cult., Snohomish Co., WA, 1995);	none	For 'Arlington' map see Native Seed Network (2004). Originated from a wild population coll. 1979 at < 100 m elevation; not intentionally bred or hybridized; selected in comparison to 128 populations from OR, WA, and other states. Not appropriate for Rocky Mountains or interior regions (Ogle et al. 2003).
Elymus glaucus Buckl. ssp. *jepsonii* (Burtt-Davy) Gould	blue wildrye	"Elkton' (cult., Douglas Co., OR, 1997)	none	For 'Elkton' map see Native Seed Network (2004). Originated from a coastal population coll. in 1979 at < 150 m elevation; not intentionally bred or hybridized; selected in comparison to 128 populations from OR, WA, and other states. Chosen for early development and uniformity. Not appropriate for Rocky Mountains or interior regions (Ogle et al. 2003).
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould ssp. *lanceolatus*	thickspike wheatgrass	'Bannock' (cult., comp. from OR, ID, WA, 1995); 'Critana' (cult., Hill Co., MT, 1971); 'Schwendimar' (cult., The Dalles, OR, 1994); 'Sodar' ("streambank wheatgrass" cult., Grant Co., OR, 1954)	'Critana' source collected in 1960 and develped by direct increase for stabilization, roadsides, airports, recreation areas, construction sites. 'Sodar' mass selected for erosion control and soil stabilization, airports, dry canals, recreational areas, grassed waterways.	For 'Bannock', 'Sodar,' and 'Schwendimar' see Native Seed Network (2004). All are from Pacific Northwest and are expected to differ genetically and be adapted to different habitats than populations in R2. Previously confused with *Pseudoroegneria spicata*. Cytogenetics work on F1 hybrids with Snake River wheatgrass (*E. wawawaiensis* J. Carlson & Barkworth) examined nature of hybrid male sterility (Jones et al. 1995). Mean chromosome pairing and pollen stainability in 'Secar' Snake River wheatgrass and 'Bannock' thickspick wheatgrass parents was significantly higher then in the F1 hybrids and mean of backcrosses (=outbreeding depression). Male sterility occurred due to some form of genetic incompatibility but not from major chromosomal rearrangements.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus* (=*Agropyron trachycaulum* (Link) Malte ex H.F. Lewis; *many other synonyms*)	Slender wheatgrass	'Primar' (cult., Beebe, MT, 1946); 'Pryor' (cult., Clarks Fork R. MT, 1988); 'San Luis' (cult., Rio Grande Co. CO, 1984);	'San Luis', selected from 1975 accession from San Luis V., Rio Grande Co., CO; increased from original collection; meant for above 1,800 m and at least 35 cm ppt.	For 'Primar' map see Native Seed Network (2004). 'San Luis' a more southern genotype for high elevations and 'Pryor' more northern with drought and salt tolerance (Ogle et al. 2003).
Festuca arizonica Vasey	Arizona fescue	'Redondo' (cult., Los Alamos NM, 1973	none	'Redondo' was collected from many plants in 1956 from a single stand in NM (release notice, Los Lunas PMC). It does not do well at low elevation.
Koeleria macrantha (Ledeb.) J. A. Schultes (= *K. cristata* auct. p.p. non Pers., *K. gracilis* Pers., *Koeleria nitida* Nutt.)	prairie junegrass, crested hairgrass	none	Barkoel ecotype from Europe.	Barkoel ecotypes, selected from collection in The Netherlands for turf, not appropriate for restoration in N. America. Alderson and Sharp (1993) suggest using source-id seed.
Leymus cinereus (Scribn. & Merr.) A. Love (=*Elymus cinereus*)	Basin wildrye	'Trailhead' (cult., Roundup MT, 1991); 'Magnar' (cult., Saskatchewan, Canada, 1979)	Source of 'Trailhead' collected from subirrigated range site in 1960 and direct increased; developed for reclamation. Source of 'Magnar' collected in 1938; selection on vigor; for livestock range forage.	'Magnar' and 'Trailhead' drought tolerant (Ogle et al. 2003). See Native Seed Network (2004).
Leymus triticoides (Buckl.) Pilger (= *Elymus triticoides* Buckl.; *Elymus condensatus* J. Presl var. *triticoides* (Buckl.) Thurb.)	beardless wildrye	'Rio' (cult., Kings Co., CA, 1991); 'Shoshone' (cult, Riverton WY, naturalized, 1980)	'Shoshone' developed from 1958 collections from a stand in WY thought to have been established in 1940s from unknown source. 'Rio' developed from direct increase of central CA source collected in 1978.	Developed primarily for stabilization and cover on wet to wet-saline sites; 'Rio' not well suited for Intermountain West (Ogle et al. 2003). Sod forming.
Nassella viridula (Trin.) Barkworth (=*Stipa viridula* Trin.)	green needlegrass	'Lodorm' (cult., Bismarck ND, 1970)	SD-93, from a commercial harvest of seed in 1962 from native grasslands in w. SD near Fairburn; mass selection and increase of ecotype.	Cucharas green needlegrass, selected class, natural track, released 2003, originally collected from Huerfano Co., CO. in 1993 (Jones & Nielson 2004). Lower seed dormancy and higher seed yield than 'Lodorm' in evaluation at Logan, UT. G3 and G4 generation seed available to growers (G5 prohibited). Some loss of seed dormancy and seed shattering likely.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Panicum virgatum L. Two varieties in R2: 1) *P. v.* var. *virgatum*; 2) *P. v.* var. *spissum* Linder	switchgrass	Lists 9 cultivars, 1 informal, 3 source-identified, and 1 germplasm release. In R2: 'Forestberg' (cult., Sanborn Co., SD, 1987); 'Nebraska 28' (cult., Holt Co., NE, 1949)	Lists 15 cultivars, 4 from R2: 'Nebraska 28', source collected in Holt Co, NE in 1935; spaced plants allowed to open-pollinate; seed bulked and increased. 'Pathfinder', source from 1953 collections from NE and KS; planted in nurseries and polycrossed; 12 superior clones selected; further selection and intercrossing. 'Summer', coll. s. of Nebraska City, NE, 1953; mass selection for earliness, leafiness, rust resistance. 'Trailblazer', hexaploid ($2n = 6x = 54$), single-plant selections based on digestiblity from nursery planted in 1973; established high and low digestibility nurseries and further developed as pasture grass.	There are distinct differences among cultivars. For example, flowering of 'Dakoth' is 27 days earlier than 'Forestburg' and 45-50 days earlier than 'Cave-in-Rock', 'Summer', 'Pathfinder', and 'Nebraska-28' (Alderson and Sharp 1993). *Differences in maturation time can be critical to success in different environments and to interactions with other species.* 'Blackwell' developed from seed from 1934 collection from single plant in native prairie near Blackwell OK (Alderson & Sharp 1993). *Expect serious constriction of genetic variation and homogeneity.*
Pascopyrum smithii (Rydb.) A. Löve (=*Agropyron smithii* Rydb.)	western wheatgrass	'Arriba' (cult., Kit Carson Co. CO, 1973); 'Barton' (cult., Barton Co., KS, 1970), ND-WW093 (germ., ND & SD, 1993); ND-WWG932 (Germpl., Alberta & Saskatchewan, Canada, 1993); 'Rodan' (cult., Morton Co. ND, 1983); 'Rosana' (cult., Rosebud Col, MT, 1972)	Lists 10 cultivars, 4 incl. R2: 'Ariba' (spelling error?), coll 1957 near Flagler, CO at 1,530 m, ppt. 40 cm; bulk increase from initial planting. 'Barton', from seed coll. In 1947 from clay bottomland, Barton Co., KS; field increased and tested as PM-K-402; strongly rhizomatous ecotype. 'Flintlock', selection from 30 accessions coll. in 1957 from central and southwestern NE and northwestern KS; recurrent selection for forage, seed yields, and rhizome production; aggressive vegetative spread. 'ND-WWG931', selected from vegetative samples of 5,140 genotpes in 1977 from 1,028 sites in western ND and SD; recurrent selection for vigor, rhizome spread, leaf density, seed production for abandoned cropland and rangeland.	Early selections, including 'Flintlock,' may be too aggressive for restoration.
Poa alpina L.	Alpine bluegrass	'Greuning' (cult., France, 1979)	'Greuning' mass selected from material originally collected from near LaCure, Switzerland.	No R2 or regional US releases.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Poa secunda J. Presl (current treatment lumps all former forms, varieties, subspecies, and species in *P. secunda*/*P. scabrella* complex-see Table 10.1). Former cultivars based on names and forms as follows: 1) *P. sandbergii* Vasey 2) *P. ampla* Merr. 3) *P. canbyi* (Scribn.) T.J. Howell)	1) Sandberg bluegrass 2) big bluegrass 3) Canby bluegrass	1) High Plains Germplasm (comp. from MT and WY, 2000) 2) 'Service' (cult., Yukon Ter., Canada, 1990); 'Sherman' (cult., Sherman Co. OR, 1945) 3) 'Canbar' (cult., Columbia Co. WA, 1979)	1) none 2) 9005460, from black alkali site, near Laramie, WY, direct increase of original collection. 3) none	1) Larson et al. (2001) found distinctive AFLP patterns (scored band presence or absence) among 'Sherman', 'Canbar', and two natural populations of Sandberg bluegrass. Shannon-Weaver diversity index values of 19.5, 21.8, 4.8, and 0 for the two Sandberg populations, Canbar, and Sherman, respectively. Variation in natural Sandberg bluegrass populations was similar to the dioecioius *P. fendleriana*. Both species can produce apomictic seeds (Kellogg 1987). 2) 'Service' selected from collection from Yukon Terr., Canada; 'Sherman' developed from mass selection of 1932 and 1935 collections from Sherman, OR (Alderson and Sharp 1993, Larson et al. 2001). Sherman composed of a single genotype (Larsen et al. 2001). 3) For 'Canbar' map see Native Seed Network (2004). Apomictic grass collected from Blue Mountains, WA. Composed of very few genotypes (Larson et al. 2001). Canbar is highly competitive with cheatgrass (*Broumus tectorum*) (Pullman PMC, release notes). *Planting of Canbar or Service could erode genetic diversity of populations.*
Pseudoroegneria spicata (Pursh) A. Löve ssp. *inermis* (Scribnl. & J. G. Smith) A. Löve (= *Agropyron inerme* (Scribn. & J.G. Sm.) Rydb.)	beardless wheatgrass (bluebunch wheatgrass)	'Whitmar' (cult., Whitman Co. WA, 1946)	none	For 'Whitmar' map see Native Seed Network (2004). Diploid. This species complex has complex cytogenetics and hybrid incompatibilities.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Pseudoroegneria spicata (Pursh) A. Löve ssp. *spicata* (= *Agropyron spicatum* (Pursh) Scribn. & J.G. Sm.)	bluebunch wheatgrass	'Goldar' (cult., coll. Aberdeen ID, 1989)	Note: 'Goldar' included here because was used in development of 'P-7'. Goldar (selected from native plt. Collection, Malley Ridge, Umatilla Natl For, Asotin WA, 310-473m, open ponderosa pine woodland, 1934).	For 'P-7', 'Antone', and 'Goldar' maps see Native Seed Network (2004). P-7 (developed by ARS) is a polycross of 25 accessions from 6 states and B.C. Canada, including 'Goldar' and 'Whitmar', mostly diploid populations, and a tetraploid population, (Larson et al. 2000). Goldar and Whitmar are diploid cultivar releases of two different subspecies. Competition studies were done between 'Goldar' and diffuse knapweed compared under different conditions in a growth chamber (Larson and Kiemnec 2003) to examine if cultivar can out compete invasive species, but did not examine effect of cultivar on native species or on native genotypes. Goldar tested against > 1000 accessions (Gibbs et al. 1991).
Schizachyrium scoparium (Michx.) Nash	little bluestem, Pastura	'Aldous' (cult., Flinthills KS, 1966); Badlands ecotype (sel., ND and SD, 1996); Central Iowa Germ (source-id, composite from northern IA, 1999); 'Cimmaron' (cult., eastern KS & OK, 1979); Itasca Germ (sel., ND SD MN, 2001); Norhern Iowa Germ (source-id, composite from northern IA, 1995)	'Aldous' composite of multiple accessions coll. in 1935 from Flint Hill s. of Manhattan KS; tested after several generations of selection. 'Camper' from accessions in 1953 from NE and KS; bred from 2 unrelated lines selected for leaf color. 'Cimarron' from many accessions from KS and OK in 1959 from 750-1,075 m, 38-50 cm precipitation, bulked for seed increase; selected for harvest uniformity with combine, intended for range and disturbed areas.	None of the cultivars are appropriate for restoration.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Sorghastrum nutans (L.) Nash	indiangrass	Lists 6 source-identified releases, 5 cultivars, and one informal release. Two are from R2: 'Osage' (cult., KS and OK, 1966); 'Tomahawk' (cult., ND and SD, 1988)	Lists 11 releases, including 3 cultivars from R2. 'Osage' developed from seeds collected in 1953 from central KS and Oklahoma for range and pasture reseeding. Recurrent selection for leafiness, vigor, lack of rust, early flowering. Narrowed down to 8 clones. 'Tomahawk' (Reg. No. CU-131) is a composite of three seed collections from native stands from Dickey and Marshall Cos., ND and Brown Co, SD. Compared to 16 other accessions at Bismarck PMC. Selected for high seed yield and winter survival. Intended for combination of range, pasture, wildlife habitat, natural areas, and erosion control, and mine revegetation. 'Holt' (released 1960) grown and mass selected for range and pasture reseeding at Lincoln NE since 1942 from seed collected in Holt Co., NE.	There is a large range of maturation time among cultivars and native populations of this wide-ranging species that might affect community interactions or ability to produce seeds in particular habitats. For example, 'Tomahawk' matures 33 days earlier than 'Holt', 71 days earlier than 'Oto', and 82 days earlier than 'Osage' and 'Rumsey' (Alderson and Sharp 1993). The species is a self-incompatible polyploid (Gustafson et al. 2004a), and therefore highly outcrossing. Chromosome number is invariable and not likely to play a role in crossing success (Keeler and Kwankin 1989).
Herbs and subshrubs:				
Artemisia ludoviciana Nuttall	Louisiana sage (has races, ssp.)	'Summit' (cult., Fear L. Co. ID, 1986)	none	'Summit' was selected from a strain chosen for ability to establish on harsh sites, control erosion, and encourage establishment of "higher plant forms" (=nurse plant) (release notes, Meeker PMC). Collected in 1975 at 1,909 m in MLRA "Northern Rocky Mountains." Tested well at mid elevations in ID, WY, CO, and UT. Ogle et al. (2003) note it was selected for vigorous rhizome activity.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
***Chamaecrista fasciculata* (Michx.) Greene** (= *Cassia fasciculata* Michx.); Two varieties: 1) *C. f.* var *fasciculata* 2) *C. f.* var. *macrosperma* (Fern.) C.F. Reed	partridge pea, sleeping plant	'Comache' (cult., TX, 1985); Lark Selection (sel., AR, 1997); Riley Germplasm (source-id, KS, 1999)	none	Riley Germplasm is recommended for wildlife habitat improvement, roadsides, parks, recreation areas, and beautification (showy yellow flowers). The species has no invasive qualities. It is a colonizing pioneer species. Original collection was from a roadside in KS in 1977 in USDA Hardiness Zone 5b (release notice and flyer, Manhattan PMC). See Table 10.1- 10.5 regarding local adaptation, inbreeding depression, and outbreeding depression in this species. Distant translocation of populations (such as across hardiness zones) can lead to significant decreases in survival and reproduction following hybridization with local stands (e.g., Fenster & Galloway 2000, Etterson 2004a, b). See Tables 10.4-10.5.
Dalea candida Michx. Ex Willd. 1) *D. c.* var. *candida* 2) *D. c.* var. *oligophylla* (Torr.) Shinners	white prairie-clover	Antelope germ. (tested, Dickenson, ND, 2000)	none	Antelope germplasm was collected in 1947 in ND, subjected to evaluation and sent to Bridger, MT for further development in 1960. Intended for diverse purposes, including reclamation (e.g., strip mine sites) and conservation areas (release notice, Bismarck PMC). Evaluated as not aggressive.
Dalea purpurea Vent.; two varieties: 1) *D. p.* var. *purpurea* *2) D. p.* var. *arenicola* (Wemple) Barneb	purple prairie-clover	Bismark Germplasm (sel., SD, 2000); Central Iowa Germplasm (source-id, centr. IA comp., 1998); 'Kaneb' (cult., Riley Co. KS, 1975)	none	Bismark Germplasm (selected natural track) originated from one pound of seed collected in 1975 in south central SD (Bismark PMC). Not invasively aggressive. Accession selected based on superior vigor, above average seed yield, and abundant foliage in northern areas. 'Kanab' adapted to central portion of species distribution. Originally collected in 1948, increased first at Manhattan, KS, then at Los Lunas PMC, then tested in multiple locations before release.

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Helianthus maximiliani Schrad.	Maximilian sunflower	Medicine Creek Germplasm (sel., SD, 2000); 'Prairie Gold' (cult., KS, 1978); 'Aztec' (cult., TX, 1978)	none	Medicine Creek germplasm, selected class (natural track) released from Bismark PMC in 2000. Clonal by spreading rhizomes. Originated from only 6 vegetative samples from site in central SD (Hughes Co.) at about 500 m. Replaces use of southern releases that failed to flower in northern states. Flowering and seed maturation 2-3 weeks earlier than ND accessions.
Linum lewisii Pursh	blue flax (Lewis flax)	not 'Appar' (Appar is *L. perenne*)	none	Maple Grove Germplasm is the only current release of native *L. lewisii*. It is selected class germplasm developed by USDA Forest Service and Aberdeen PMC (Ogle et al 2003). 'Appar' was developed from naturalized populations of the European *Linum perenne* L. and should not be mistaken for a native cultivar.
Penstemon strictus Benth.	Rocky Mountain penstemon	'Bandera' (cult., Torrance Co. NM, 1973)	none	No R2 releases. 'Bandera' was released for use for beautification of high-way medians, rest areas, and roadside stabilization plantings (Release Notes from Los Lunas PMC, Hooks & Oaks 1982). Used in ornamental landscaping. Original seed collected in 1964 at a campground in Cibola National Forest, NM, at about 2,225 m. Seed direct increased. No assessment of genetic diversity. This cultivar is used for highway plantings in R2. Not evaluated for restoration. Bandera from mid-elevation has low primary seed dormancy, but seed collected from high elevation site in UT had high seed dormancy (Meyer & Kitchen 1994). *Beware of using low seed dormancy cultivar in native sites where seed dormancy is sm important adaptation.*

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Sphaeralcea coccinea (Nutt.) Rydb.	Scarlet globemallow	—	none	Registered germplasm: ARS-2936 Scarlet Globemallow Germplasm (Rumbaugh et al. 1993, listed as S. c. (Pursh) Rydb.). OK to use as pre-varietal germplasm. Showy red flowers anticipated as good for highway and garden plantings. Widely spreading rhizomes. Collected in n. ID in 1987 and compared with other species of globemallow. Selected because highly palatable to livestock.
Shrubs:				
Amelanchier alnifolia (Nutt.) Nutt. Ex M. Roemer	Saskatoon serviceberry	Kendrick Germ. (sel., Deary, ID, MLRA B-9, 2000); Newport Germ. (sel., Newport, WA, MLRA E-44, 2000); Okanogan Germ. (sel., Okanogan, WA, 2000)	none	These are rhizomatous shrubs with massive rootcrowns. Newport germplasm is *A. l.* var. *alnifolia and* represents three plants from an original six plants (release notice, Pullman PMC). Okanogan germplasm represents five of an original six plants. *This is very low genetic diversity and is a severe bottleneck.*.
Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle	(=mountain sagebrush on Monsen list)	'Hobble Creek' (cult., Springille, UT, 1987)	none	'Hobble Creek' selected for mule deer and domestic sheep winter ranges (release notice Meeker PMC). Collected in 1968. A distinct ecotype.
Atriplex canescens (Pursh) Nutt.	fourwing saltbrush	'Marana' (cult., San Diego Co., CA, 1979); Snake River Plains Germ (sel., comp. from ID, 2001)	none	Another cultivar, 'Rincon' released in 1982 was originally collected in 1957 from Rio Arriba Co., NM at 2380 m for forage and cover in big sagebrush and pinyon-juniper zones. More cold tolerant than 'Marana'. 'Marana' is only appropriate for warmer Mediterranean zone (release notice). Seeds used to develop 'Marana' were collected in 1961 in inland San Diego Co., CA at 182 m elevation. Seeds increase was done in Pleasanton PMC in containers, then tested at 30 sites throughout CA (Lockeford PMC).

Table 8.2. Continued.

Species	Common name	Englert et al. 2002 (release type, where collected, year released)	Alderson and Sharp 1993 (notes about releases)	Additional comments
Cercocarpus montanus Raf.	Mountain mahogany; Mule Deer seed Mountain mahogany	'Montane' (cult., Coyote, NM, 1978)	none	'Montane' was selected for commercial production and sale of seed and plants (Release notice. Seed collected in 1964 in Santa Fe National Forest. Increased by irrigated plantings. Tested in CO and NM. Direct seeding in wildlands yields poor results. Use in irrigated locations outside adaptive zone.
Purshia tridentata (Pursh) DC	bitterbrush, Antelope bitterbrush	'Lassen' (cult., Lassen Co. CA, 1984); Maybell Source (sel., Moffat Co. CO, 1997)	none	'Lassen' is a tall growing ecotype selected for improving forage on big-game and winter ranges (Lockeford PMC, Shaw & Monsen 1986). Originally collected from stands near Janesville, Lassen Co., CA. at ~ 1,265 m. Tested in n.e. CA, UT, NV, ID, OR and recommended for Intermountain and Pacific Northwest regions. Maybell Source select class germplasm is a unique, low-growing, creeping or decumbent selection with poor post-fire resprouting ability and a propensity for layering meant for rangeland reclamation (release notes, Meeker PMC). Seed originally collected in 1982. *This distinct decumbent form is not meant for ecological restoration.* (Appears to also be called Waybell Source.)
Rhus trilobata Nutt.	skunkbush, skunkbush sumac	'Autumn amber' (cult., Littlefield TX, 1983); 'Bighorn' (Cult., Basin WY, 1979)	none	'Autumn amber' was selected and released based on its brilliant fall color and low growth habit (release notice, Los Lunas PMC). Selected on color and form from a 1957 collection in TX. The plants do not produce fruit. Propagated only vegetatively. *Autumn amber is appropriate for landscaping, not restoration or other revegetation of wildlands.* 'Bighorn' was originally collected as seed in 1957. Many genotypes lost during testing. Widely adapted for use along highway, roadside rest areas, recreation sites, and home sites (release notice, Los Lunas PMC).

Table 8.3. Example of conservation plant releases from USDA NRCS Manhattan Plant Materials Center, KS. This is a partial listing as of June 2004. These species occur somewhere in the five-states of Region 2, but not all the releases are derived from collections made within Region 2. In the column labeled "release type", "cultivar" is varietal germplasm and all others are pre-varietal germplasm. Releases before 1993 may deviate from current naming conventions (Box 11). Releases before 2000 did not require environmental assessment. Complete tables are online: http://plant-materials.nrcs.usda.gov/kspmc/about.html.

Release name	Scientific name	Common name	Year	Plant type	Release type
Kaw	*Andropogon gerardii*	big bluestem	1950	grass	cultivar
Garden	*Andropogon hallii*	sand bluestem	1960	grass	cultivar
El Reno	*Bouteloua curtipendula*	sideoats grama	1944	grass	cultivar
Texoka	*Buchloe dactyloides*	buffalograss	1974	grass	cultivar
Pronghorn	*Calamovilfa longifolia*	prairie sandreed	1988	grass	cultivar
Riley Germplasm	*Chamaecrista fasciculata*	partridge pea	1999	legume	source-identified
Kaneb	*Dalea purpurea*	purple prairieclover	1975	legume	cultivar
Reno Germplasm	*Desmanthus illinoensis*	Illinois bundleflower	1999	legume	tested
Bend	*Eragrostis trichodes*	sand lovegrass	1971	grass	cultivar
Prairie Gold	*Helianthus maximiliani*	Maximilian sunflower	1978	forb	cultivar
Midas	*Heliopsis helianthoides*	false sunflower	1984	forb	cultivar
Kanoka	*Lespedeza capitata*	roundhead lespedeza	1998	forb	cultivar
Eureka	*Liatris pycnostachya*	thickspike gayfeather	1975	forb	cultivar
Blackwell	*Panicum virgatum*	switchgrass	1944	grass	cultivar
Kanlow	*Panicum virgatum*	switchgrass	1963	grass	cultivar
Barton	*Pascopyrum smithii*	western wheatgrass	1970	grass	cultivar
Southwind	*Phragmites australis*	common reed	1998	grass	cultivar
Sunglow	*Ratibida pinnata*	grayhead prairie coneflower	1978	forb	cultivar
Konza	*Rhus aromatica* var. *serotina*	aromatic sumac	1980	shrub	cultivar
Aldous	*Schizachyrium scoparium*	little bluestem	1966	grass	cultivar
Cimarron	*Schizachyrium scoparium*	little bluestem	1979	grass	cultivar
Cheyenne	*Sorghastrum nutans*	indiangrass	1945	grass	informal
Osage	*Sorghastrum nutans*	indiangrass	1966	grass	cultivar
Atkins Germplasm	*Spartina pectinata*	prairie cordgrass	1998	grass	selected
GSF- I	*Tripsacum dactyloides*	eastern gamagrass	1984	grass	germplasm
Pete	*Tripsacum dactyloides*	eastern gamagrass	1988	grass	cultivar
PMK- 24	*Tripsacum dactyloides*	eastern gamagrass	1974	grass	germplasm

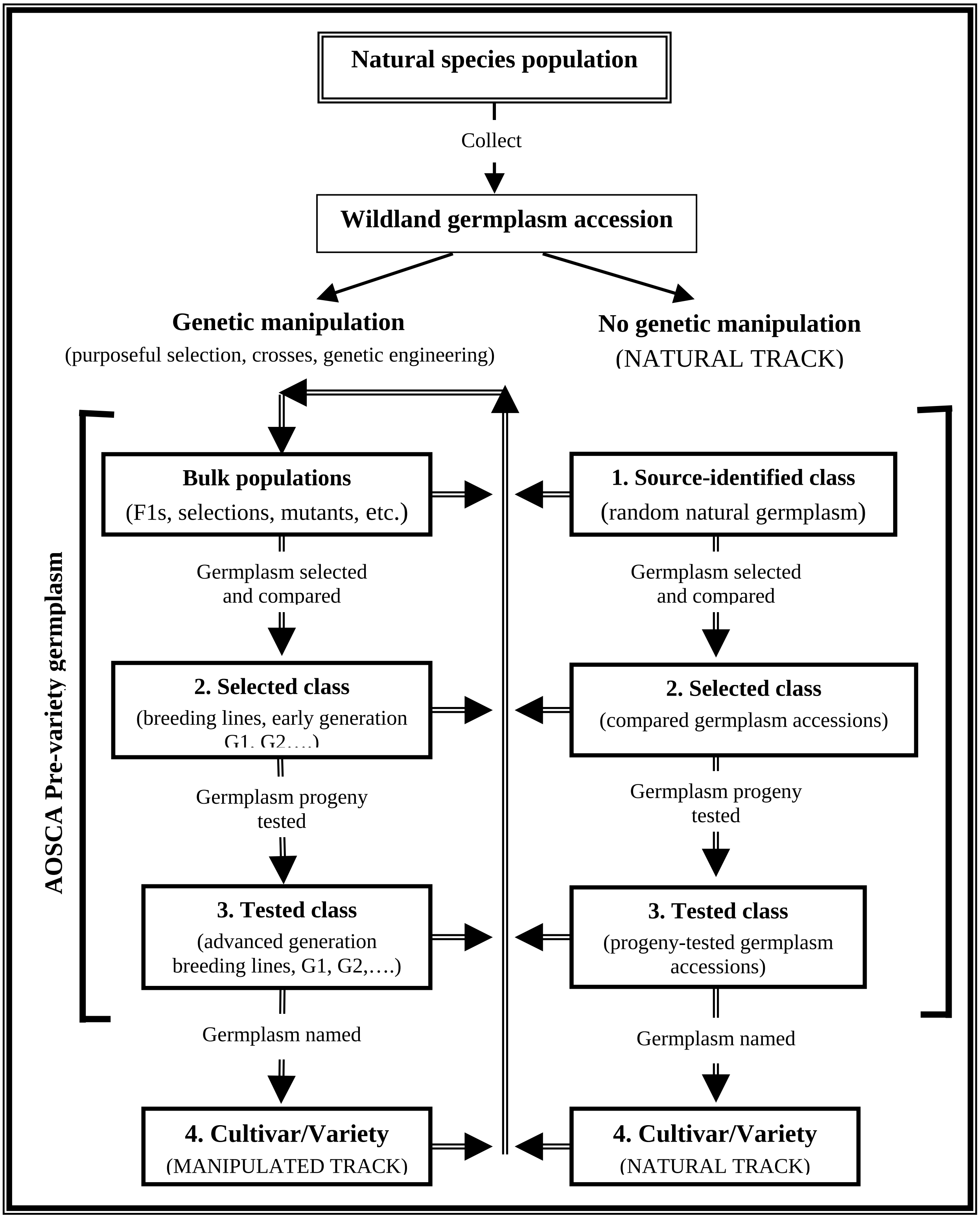
Table 8.4. Example of procedures that could minimize genetic bottlenecks and unintended genetic shifts in native plant collections and releases. This table is for non-tree species. Collection and production of plant materials appropriate for ecological restoration require special care to prevent sampling bias, genetic erosion, and unintentional selection. Different agencies have different protocols. Currently, release notices provide little to no information about protocols used to collect germplasm. If collection protocols were included in release notices, then it could be determined if collection standards were achieved in practice. Deviations could be reported in release notices to better inform the public about the release. Main references: Marshall and Brown 1975, Brown and Briggs 1991, Meyer and Monsen 1992, Knapp and Rice 1994.

Activity	Procedure	Comments
Seed collection	Many individual plants per population collected (> 200) are preferred. To capture diversity of sampled population, vegetative samples require higher sample numbers than when multiple seeds are collected from individuals. Larger sample numbers are needed from inbred than outbred species. Sample > 10 propagules/plant whenever possible.	~200 samples may be needed to maintain allelic frequencies similar to the original population (Marshall & Brown 1975). A minimum of ~ 30-60 are required to capture an average of 95% of the variation in outbred population.
	Seeds or other propagules from each individual plant collected and maintained separately if for container stock, plantation, or genetic studies. Bulk-collect for seed increase or direct seeding.	Family identity of seeds valuable for genetic studies. Different mothers can always be bulked later.
	Collect seed or vegetative samples from randomly selected individuals using a minimum spacing criterion. Systematically sample across the population. Avoid plants with smut or obvious disease.	Stratified random sampling captures spatial variation created by limited dispersal and patchy distribution of genotypes (Brown & Briggs 1991).
	For herbaceous plants set minimum spacing of samples according to size, density, continuity of populations, and biology of species sampled. Use larger spacing for larger, low density plants or spreading clones (~ 20 - 100 m) than for very small, non-clonal, high density plants (minimum of ~ 5 - 20 m). For trees and shrubs, the Seed Handbook (US Forest Service 1993) requires minimum of 200 ft. between samples.	If stands are patchy and discontinuous, collect from multiple stands in the same area within 500 ft. elevational band. The distance of 200 ft. between samples could be shortened for many, non-clonal, outcrossing shrub species and most herbs, especially if they grow at high density.
	Collect seeds on enough dates to avoid selection against either early or late maturing genotypes.	Match the collecting to the distribution of maturation.
Seed increase – 1st generation	Sufficient stratification, scarification, smoke, heat, or other treatment to break dormancy of all or most seeds.	Seed dormancy is an important adaptive trait.
	Establish plants from an equal number of seeds from each plant collected.	
	Grow the plants so as to minimize inter-plant competition	
Number of generations	Few (no more than 1 is preferable)	
Seed increase location	The location should be environmentally similar to the original collection site.	This is more critical as the number of generations increases
Harvest practices	Harvest seed in a way that captures the distribution of maturation and flowering times represented in the population. This may require more than one collection date. Develop harvest methods that capture seeds that shatter rather than selecting against seed shatter.	For seeds that shatter or fruits that have ballistic release of seeds, develop collection technique that minimizes selection of non-shattering forms (e.g., Burton & Burton 2002).

Table 8.5. Questions relating to commercial plant materials. The project is assumed to be post-fire or post-harvest. A separate set of comments would be relevant to different levels of highly degraded sites. Mindful attention to these questions can help guide choices of genetically appropriate plant materials for natural areas. Many risks now evaluated by PMCs during development of plant materials (NPMM 2000). The risks mentioned below are not included in the rating system for environmental evaluation of NRCS plant material releases.

Question	Cause for confidence	Cause for concern	Comments
How was original germplasm collected?	Many plants per population or local ecoregion and well distributed over population	Few plants, plants from mix of widely differentiated populations, mixed cytotypes.	Collection procedure and minimum number of plants sampled per population depend on mating and breeding systems and patterns of genetic differentiation; avoid collections with high potential for genetic bottleneck or genetic erosion. Accession best if > 60-200 well-spaced samples.
Was collection location well documented?	Yes; it is appropriate for project site	No	Avoid materials that have poor documentation or that are from inappropriate sites
Were the seeds tested for purity and viability?	Yes; it is high (or if low, the sale is based on pure live seeds)	No	Avoid materials that have no seed test
Were the seeds tested for weed content?	Yes, there are no noxious weed species and non-targeted species minimal	No	For direct seeding, avoid seedlots that have not been checked for seeds of noxious weeds; reject seedlots that contain noxious weeds or other problematic species
How many generations of seed increase?	1	> 1	Reject if adaptive traits likely to be lost/ altered; allow more generations if unintentional selection and genetic erosion minimized.
Isolation distances in seed increase fields sufficient to assume low or no hybridization with other crops or natural populations?	Yes	No, there is risk of hybridization with nearby crop of same or related species, or native bordering populations.	Acceptable levels of risk should be low (for example, < 2% of seeds sired by outside production field); if progeny tests show no potential for outbreeding depression after 3 generations of crosses, then higher levels of "genetic pollution" of crop may be acceptable.
Were differentiated populations mixed during field increase?	No	Yes, there is risk of outbreeding depression or formation of new aggressive genotypes	Risk needs to be assessed in light of potential for inbreeding depression. Risk of outbreeding depression and new aggressive genotypes can be reduced if mixed populations are closely related (low genetic distance) and from similar habitats.
Were risks involving species interactions evaluated (e.g., competitiveness and hybridization potential)?	Yes, genetically manipulated release no more aggressive than resident populations; species not likely to hybridize with sensitive species.	No	Unknown risks are problematic; aggressiveness, invasiveness, large shifts in timing of growth, hybridization with rare species, genetic assimilation, all have potentially cascading effects through native communities. Request risk evaluation research for major restoration species.

Figure 8.1. AOSCA seed certification guidelines and nomenclature for release types in the genetically manipulated versus natural development tracks (after NPPM 2000, Exhibit 540-34). Of all release types, the natural track, pre-variety classes most resemble the natural population.



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Additional Resources

NRCS-PMC 2004. To get click-on list of Plant Materials Centers and lists of publications and plant releases go to: http://plant-materials.nrcs.usda.gov/centers/index.html.

The following five USDA-NRCS Plant Materials Centers cover most of Region 2:
Bridger, MT (for northern WY): http://plant-materials.nrcs.usda.gov/mtpmc/about.html.
Meeker, CO (Rocky Mountains of w. CO and s. WY):
http://plant-materials.nrcs.usda.gov/copmc/about.html.
Manhattan, KS (most of KS and NE): http://plant-materials.nrcs.usda.gov/kspmc/about.html.
Bismarck, ND (SD and nw NE): http://plant-materials.nrcs.usda.gov/ndpmc/about.html.
Los Lunas, NM (eastern plains of CO): http://plant-materials.nrcs.usda.gov/nmpmc/about.html.

Great Basin Research Center, Utah, Seed Resources. Online:
http://www.wildlife.utah.gov/gbrc/seedresources.htm.

Great Basin Native Plant Selection and Increase Project 2002 Progress Report. Online:
http://www.wildlife.utah.gov/gbrc/greatbasinplantselection.htm.

RNGR 2004. USDA Forest Service Reforestation, Nurseries, and Genetics Resources provides an online National Directory of Plant Material Providers. Search for plant materials by state, product, or a keyword: http://www.rngr.net/nurseries/plant_directory.

Box 10: Wildland Seed Certification Programs

By the early 1990s, the need for native plant seed to restore wildland habitat had grown substantially as had concern about the shortage of native plant seeds from documented locations. Not only was it difficult to obtain the quantities of native shrub, grass, and forb seeds needed, but also the tracking systems used by many collectors did not assure the identity of wildland source locations. Seed users wanted to be sure they could obtain seeds appropriate for their project sites, and seed businesses wanted a way to fill the growing demand for wildland germplasm. A system was needed to promote an increase in wildland seed availability along with assurances about the quality and source-identity of the seeds. The concern inspired corrective action.

In 1993, a consortium of representatives from Utah's land management agencies, seed certification agency, seed testing laboratory, private seed industry, and the research community formed the Utah Interagency Plant Materials Committee. They worked together to develop guidelines for a tracking and certification system for wildland seed accessions and seeds increased from native wild accessions (Kitchen and Young 1995). Both sexual and asexual germplasm were covered, but unlike past programs for trees, all life forms of seed plants were included. Their guidelines formed the basis for rules by the Association of Official Seed Certifying Agencies (AOSCA) for a seed certification program for "natural track" germplasm of wild-collected native species (Young et al. 1995). The program, first offered through the Utah Crop Improvement Association (UCIA 2003), was used as a model to develop wildland-collected, source-identified certification programs in most other states, including Colorado, Kansas, Nebraska, South Dakota, and Wyoming. Notable programs were also set up in California, Iowa, and Minnesota. Each state has a slightly modified program. They must conform to the minimum standards set by AOSCA and Federal Seed Law, while adding any more restrictive standards required by their own state seed laws (for example, Stevens et al. 1996, Houseal and Smith 2000).

States can add other safeguards. For example, California requires a voucher specimen for each collection site. This can be important. Although all programs require submission of a seed sample from every seedlot that can also be used to authenticate collections, not all species can be told apart by their seeds. In addition to offering flexibility based on state law, AOSCA-based programs can allow seed users to add requirements that can be specified in seed collection and production contracts. For example, minimum spacing between original collections and a minimum number of sampled plants can be specified on a species-by-species basis if desired.

The system relies on accurate tracking and auditing. Genetic testing is not required. AOSCA guidelines, though not failsafe, significantly improve the reliability and quality of wildland-collected and increased seeds. For a particular accession (seedlot), the system verifies the genus, species and ecotype characteristics of the natural wildland population (in some states also naturalized populations) and documents and tracks germplasm from the time it is collected to availability for purchase. It tests for seed purity and weed seed content (no noxious weeds are allowed), limits other non-targeted seed (as regulated by states), and tags germplasm accessions that comply with the process. The process includes inspections of field sites and increase fields entered into the program, and it requires rigorous documentation. A sample of sites and fields are examined during collection and seed processing. AOSCA requires that "at least 5% of eligible seed lots, including verification of paperwork and prior and/or retroactive field inspection of collection sites to verify that stands are capable of producing the amount of seed reported from any site." States differ in the rigor of their auditing systems; they vary from 5% to 100% of sites visited. In California, all sites were confirmed by inspectors in the first two years of the program. In Colorado, at least 5% of application sites are visited by an inspector. At any time, businesses must be prepared to show inspectors that their record keeping, labeling, and seed processing procedures maximally eliminate potential errors in labeling.

The germplasm collected from the natural species population without any purposeful selection is categorized into the following three "natural track" classes of "pre-varietal germplasm" (a-c below) and a natural track "cultivar" class (d, below) (see Figure 8.1):

(a) Source-Identified (yellow tag): only the species and original germplasm collection site are known. No genetic manipulation is allowed and no comparisons (tests) with other germplasm accessions are required.

(b) Selected (green tag): Shows promise of superior and/or identifiable traits as contrasted with other germplasm accessions, ecotypes, or variety/cultivars of the species when compared at a common site.

(c) Tested (blue tag): Requires progeny testing to prove that traits of interest are heritable in succeeding generations. Testing procedures (number of sites, generations required, etc.) are outlined for each species by seed-certification agencies.

(d) Variety/Cultivar, natural track (white, purple, or blue tag, depending if foundation, registered, or certified generations): Progeny of wild-collected seeds or stands of tested parentage that have proven genetic superiority with respect to some identified standard (Ogle et al. 2001). The assemblage of cultivated plants is clearly distinguished by morphological, physiological, cytological, chemical, or other traits and retains its distinguishing characters after sexual or asexual reproduction. This condition of "proven superiority" is apparently left over from rules for regular-track cultivars and can likely be relaxed. The idea of "superiority" is subjective. In addition, use of the word "cultivar" is something of a misnomer for a natural track germplasm. In common usage, "cultivar" is used to describe a plant that has originated and persisted only under cultivation.

The natural track classes (a-c) of germplasm are the most similar to the native population/s and are preferred for ecological restoration. The source-identified class is the fastest to produce and is likely to have the most diversity in terms of numbers of different populations available for purchase. As such, the largest choice of germplasm in terms of matching proximity and environment to project sites is likely to be the source-identified class. The germplasm in these classes can be sold as original wildland germplasm (generation 0) or as a product of field seed increase (generation 1-x). Some states limit the number of generations while others set species-specific limits and remove the germplasm's natural status if at any stage it is shown that it has become significantly altered from the original collection. In such cases, the germplasm can be reclassified as "manipulated" germplasm as indicated under the "manipulated track" in Figure 8.1. If at the "cultivar" stage, there has been a genetic shift compared to the wild-collected accession, the germplasm is supposed to lose its natural track status.

In addition to the availability of seed-certification programs by each state's official crop improvement association, there are other programs available to facilitate the tracking of native plant materials. The Native Seed Network (2004c) sponsors an online network for tracking seeds from wild collection through cultivation to out-planting at project sites. Their integrated system allows project managers to find seeds that are available and appropriate for their planting sites. It also tracks collection intensity and frequency and helps identify areas for future collection. Certified seeds can be located through this site.

Wildland seed certification programs can facilitate the processing of large quantities of source-identified seeds for contracted projects. During the first few years of the California program, a local water district contracted with seed collectors to supply source-identified seeds from an ecoregion in Riverside County, California (Montalvo et al. 2002). The water district chose to use local, certified seeds for restoration of a wildlife reserve and provided a three-year window to organize the seed contracts and obtain seeds. In two years, the Crop Improvement Association with the help of the University of California, Riverside, source-identified about 175 seed lots belonging to 35 native plant species for the project. Twenty-four source-identified seed lots were planted in production fields for seed increase. In just over two years, over 35,000 lbs. of source-identified (yellow tagged) seeds were made available for the restoration project. Extra seeds were produced and subsequently sold on the open market. The price of the seeds was adjusted to cover the cost of certification.

As part of the certification process, there is a paperwork trail for tracking seeds from the time the collection site is submitted for approval through to seed collection, processing, and labeled with official yellow source-identified certification tags. There is also a written record kept of the site inspections, including source sites, production fields, and seed processing sites, as well as for the seed tests at an approved seed lab.

The purpose of the site visits is to verify the species/site information as reported by the seed collectors on their application forms. Specifically, the field inspector's goal is to verify:

- Identity of the plant species. This is done before germplasm collection.
- Location of the collection site
- Abundance of the species at the collection site. Only an approximation of abundance is required. The goal is to help the inspector to rule-out improbable quantities of collected seed from the site as reported by the collector.
- Suitability of collection sites/production fields. For example, because historically roadsides often have been seeded with off-site material, a contract may specify that only natural populations are acceptable and that collection of seed from planted roadways is not allowed. Seed-increase fields are checked for appropriate isolation distances from other fields of the same species or relatives with which they could hybridize.

For seeds collected for a particular project, detailed requirements for the suitability of collection sites and production fields can be specified in the seed collection and production contracts.

Another type of site visit, "spot inspections", serve to check on the performance and reporting accuracy of the seed collectors and to verify the identity and lot purity of a given species/site combination. Random, unannounced inspections during seed collection are made by an inspector from the seed-certifying agency. Seed collectors notify the seed-certifying agency in advance of collection to allow random checks to be made. For the California water district project, random spot checks were made on about 25% of the seed lots during seed collection, but a lower percentage may be required.

Once seeds are inspected by an approved seed lab, a seed inspection report is issued to the seed collector and seed-certifying agency. Seed must be inspected for purity and noxious weed seed content and it may be required to be tested for seed viability. Once all forms have been received by the seed certifying agency and the seed lot passes inspection, a certification tag with an ID number is issued to the seed company for the approved seedlot. Every seedlot has a unique wildland-collected tracking number. If it is intended that increased seed be certified, it is required that the planted seed be officially source-identified. Seedlots from increase fields must go through the full tracking process, including site inspections and seed testing.

Together, these procedures result in higher quality native seeds, increased accuracy of matching seeds to sites, and a growing awareness by the seed industry that buyers are willing to pay a bit more for documented seeds. Some seed producers find it pays to produce source-identified seed (Wind River 2004b) and faithfully provide certified seed to customers.

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Young, S. 1995. Alternative germplasm release procedures for producing certified seed. Seed World (July):14-15.

Young, S., S. Kitchen, J. Armstrong, and V. Watson. 1995. AOSCA approves certification guidelines for wild land collected seed. Seed World(January):20-21.

Additional Resources

AOSCA Certifying Agencies: http://www.okstate.edu/OSU_Ag/ocia/certagencies.html.

Utah Crop Improvement Association:
http://www.ucia.usu.edu/
For guidelines for permitting and certification of wildland seed, click on “certified wildland collection.” http://www.ucia.usu.edu/Certified_Wildland_Collection/Certified_Wildland.html.

Colorado Seed Growers Association
Colorado State University
Soil & Crop Sciences/Plant Science Bldg,
Ft Collins CO 80523
http://www.colostate.edu/Depts/SoilCrop/extension/CSGA/CSGA/csga.html
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Iowa Ecotype Project. 2004. Native Roadside Vegetation Center, University of Northern Iowa. http://www.uni.edu/ecotype/producers.html.

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http://www.wyseedcert.com/
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Box 11: Conventions for Classification and Naming of Native Plant Materials

It is important to understand the classification system for native plant materials used by USDA agencies and to be aware of the attributes associated with each class of plant materials. That identity provides important clues for determining how genetically appropriate the plant materials are for a project site. Here, we briefly describe the prevailing classification system used by government agencies and the seed industry and give some examples of classified materials.

The Natural Resources Conservation Service (NRCS) Plant Materials Centers (PMCs), the USDA Agricultural Research Service (ARS), and the American Seed Trade Association (ASTA) have adopted the terminology set forth by the American Association of Seed Certifying Agencies (AOSCA) for certification of plant materials. The plant materials released by federal agencies are made more available by private industry, and many of the native plant materials available in large quantities are derived from PMC and ARS releases, especially cultivars. Because of the prevalence of plant materials derived from these sources, we use terminology in this Guide that is consistent with the National Plant Materials Program and Manual (NPMM 2000).

Once native plant germplasm is collected, it can enter either the "natural track" or the "manipulated" track (Figure 8.1) for further processing and development according to AOSCA guidelines. A comparison of the various classes of wildland-collected plant materials is laid out in Table 8.1. Any of these classes of germplasm can be "released" to the public for use or for commercial development. The criteria used to determine if a plant material is appropriate for release and the number of generations the material is allowed to be grown (by Federal Seed Law) and still receive the certification status are shown in the table. In addition to the classes of seeds in the table, there are other terms associated with the classification of native plant germplasm that are useful to understand.

Wild-collected germplasm (= wildland-collected). Includes seeds and other propagules that have been collected from natural populations. Germplasm accessions collected by PMCs and other federal agencies are carefully documented. Depending on the agency and year collected wild-collected seed may or may not have followed a standard for seed sampling. Private industry germplasm is not consistently documentted as to collection standards or source. Plant material collected by private industry or government agencies can go through a certification process that assures rigorous documentation (Box 10).

Certified germplasm. Certification of native plant materials through the AOSCA program (Box 10) implies the source population was a natural population native to the site. There are two tracks for certifying wild-collected germplasm. The natural track does not allow genetic manipulation of any kind, including for example, purposeful selection, crosses, or genetic engineering (no genetically modified organisms, GMOs). Within the natural track, there are three classes of pre-varietal germplasm that can be certified (source-identified, selected, and tested) and one class of varietal germplasm (cultivar—natural track). The second track is for genetically manipulated germplasm and contains two certifiable classes of pre-varietal germplasm (tested and selected) and one class of varietal germplasm (cultivar). Germplasm in this manipulated cultivar class can be highly selected and very different from natural populations, in both behavior and community interactions. All native cultivars developed prior to AOSCA seed certification are manipulated track cultivars. Of all these classes of germplasm, plant material under the natural track will be the most similar to the local, wild population from which it was derived. Within tracks, the more generations of field increase, the less similar the germplasm will be to the parental population. If at any time germplasm in the natural track has been influenced by purposeful or significant unintentional selection, it must be removed from the natural track and rejected or placed into the manipulated track.

Released Plant Material. All of the certified classes of plant materials mentioned above, as well as other wildland derived germplasm can be released to the public if the germplasm satisfies standards set forth by the agency. Germplasm is "released" and made available to the public, according to an established standard, for a conservation purpose (Ogle et al. 2001). Often, tested and selected classes of germplasm in the manipulated track are not released.

Pre-varietal and varietal germplasms have different naming conventions. Natural track classes of germplasm (source-identified, selected, tested, and cultivar) are designated as such on a certification tag and when the germplasm is released and registered. All pre-varietal germplasm is currently named according to a binomial convention (names prior to 2000 are a bit variable in format). The first part is the descriptive name, and the second part is the fixed term "germplasm" (see Table 8.3). For example, Ribstone Indian ricegrass germplasm [*Achnatherum hymenoides* (Roem. & Schult.) Barkw] is a selected class (genetically manipulated) of certified germplasm released in 2003 (Jones et al. 2004). Varietal germplasm (cultivar) is named according to *The 1994 International Code of Nomenclature for Cultivated Plants* (Trehane 1995). The code no longer uses the term "cultivar" and "variety" as synonyms. The term "variety" is reserved for a natural taxonomic level below species.

> "*The international term cultivar denotes an assemblage of cultivated plants that is clearly distinguished by any characters (morphological, physiological, cytological, chemical, or others), is uniform in these characteristics, and when reproduced (sexually or asexually), retains its distinguishing characters*" (NPMM 2000).

Cultivar names are not italicized, and are indicated by single quotes at first use, or the word cultivar (but not both). The abbreviation cv. is properly used only with a binomial name: Genus species cv. cultivar name. Omit the abbreviation if single quotes are used: Genus species 'cultivar name'. For example, *Pascopyrum smithii* 'Barton' is a cultivar of western wheatgrass developed from a sample of seeds collected in Barton Co., KS in 1946 (Alderson and Sharp 1993), and could also be written as, *Pascopyrum smithii* cv. Barton.

Literature and Further Reading

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Jones, T. A., D. C. Nielson, S. A. Young, and A. Phan. 2004. Registration of Ribstone Indian Ricegrass Germplasm. Crop Science 44:1031-1032.

NPMM. 2000. National Plant Materials Manual (NPMM), Third Edition, June 2000. USDA Natural Resources Conservation Service, Title 190. Government Printing Office, Washington, D.C. Online: http://plant-materials.nrcs.usda.gov/intranet/manual.html.

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Chapter 9

Choosing Appropriate Genetic Sources

Choosing appropriate genetic sources for a revegetation project is not the first decision. Before arriving at this stage, one has already answered these questions:

- What will happen if we do nothing?
- Is revegetation needed or are other measures more appropriate?
- What are the revegetation objectives?
- What species, or mix of species, is appropriate for this project?

The objectives that are addressed specifically with the guidelines in this chapter and within this Guide are those pertaining to maintaining natural levels of biodiversity and a healthy functioning ecosystem. As indicated in Chapter 1, there are many reasons for making the best possible genetic decision in the service of these objectives. And, as indicated in Chapter 7, there can be serious consequences when those decisions are not well considered. It is also important to consider the longer term and evolving goals for the site, as well as the values of adjacent sites or any areas that are within possible gene flow distance (pollen or seed dispersal) of the project site. Thus, it seems well advised to not only focus on the immediate objectives of the project but possible future objectives and also on protecting the diversity and ecosystem values of adjacent sites.

Although choosing species for revegetation purposes is a topic largely outside the scope of this Guide, it is important to recognize that genetic goals are not necessarily always best served by choosing a native species. Although a native species is usually the logical choice for revegetation on Forest Service lands, *any* native species is not necessarily more appropriate than *any* non-native species, depending on the circumstances and project objectives. For example, choosing an ill-adapted population as a source of a native species may genetically contaminate neighboring plant populations, thereby undermining not only the success of the restoration project but the long-term viability of neighboring populations. Or choosing a non-local invasive cultivar of a native species that is too aggressive may result in changes in the relative abundance and composition of native species on the site, over time. Alternatively, certain non-invasive non-native species may serve important roles in reconditioning degraded sites, preparing the area for a subsequent planting of a genetically appropriate source of a native species. There is no science-based rationale for *always* choosing native over non-native species: the particular selections within species, in combination with site conditions and management objectives, will determine the most appropriate choices. See Boxes 6 and 7 for some additional information and references concerning species selection. Genetic considerations can also be important to the process of building appropriate plant palettes. For example, if a taxon is being considered for planting at a site where it does not normally occur and the site is home to another taxon with which it can hybridize, then there is reason to reconsider the choice of species.

It will not be always practical to make species-specific, project-specific seed source decisions. The need for genetic materials is not always predictable—in location or scale—and this limits the ability to apply comprehensively all available genetic information and principles. The need is understood and appreciated for generalizations, both in planning for revegetation projects and in implementation. The following guidelines are provided in the spirit of:

- Better making use of genetic principles and science-based information when there are those opportunities (time and other resources) to do so;
- Offering some suggestions for situations where seed transfer rules don’t currently exist; and
- Providing a science-based influence that may gradually lead to improvements in making genetic choices by changing expectations and encouraging all those involved in such decisions to be considering the basis for the decision. This increased awareness and participation in the genetic source decision can be beneficial, if it results in improved records about the source of planting materials used in projects. Improvement in record keeping would allow better connection between planting success/failure by seed source, and provide feedback that will positively influence decisions in the future. Specific and detailed records about genetic sources will also provide the opportunity for re-evaluating these choices in the future in conjunction with genetic monitoring.

Relationship with existing seed zone designations for Region 2

The current Forest Service Seed Handbook for Region 2, FSH 2409.26f, (USDA Forest Service 1993, hereafter referred to as the FSH) is under revision as a consolidated handbook with Regions 1-4). The FSH provides seed transfer rules for woody plants. Those seed transfer rules are based on available genetic information for adaptive traits for each species. Where no such data exist, the seed zones in Region 2 follow the former Soil Conservation Service (SCS) seed zone designations (Cunningham 1975). As better genetic information on adaptive traits becomes available, seed transfer rules are revised. There is an evolution of defining seed transfer from seed zones where one size fits all species, to customized seed zones for individual species, as new data become available: both of these zone approaches are two-dimensional in scope. As more genetic data become available on patterns of genetic variation for adaptive traits, seed transfer rules are refined using regression or climate-based models. These are typically three-dimensional in scope and are packaged as seed transfer expert systems or GIS layers in ARCINFO (M. F. Mahalovich, pers. com.).

The guidelines presented here are consistent with the FSH seed transfer rules. However, they differ in several respects. The guidelines provided here:

1. Do not create hard boundaries for seed collection or usage: rather, they allow site-specific decisions based on the most recently available information.
2. Are a companion document to the woody plants seed handbook (FSH 2409.26f) for woody species, and provide a means of making science-based choices on genetic source of material for nonwoody plant species that are not covered by current USFS handbooks such as forbs and grasses.
3. Provide a means of refining considerations in addition to FSH seed zones when there are opportunities (time and other resources) to make project-specific collections. May include some additional biological information that, while insufficient to warrant changes in the seed transfer rules or new interim directives, may nevertheless assist in understanding the species and be supportive in making appropriate genetic choices.
4. Extend beyond traditional FSH seed transfer rules by regularly considering potential effects of hybridization of translocated and resident populations. (When this information is sufficiently conclusive, it can be incorporated into the FSH as an interim directive, pending revision of the FSH.)

Caveats and general messages

These guidelines are offered to help make informed choices, and thus are presented as sets of considerations and rationale. Two important companion activities for genetic decision-making are: 1) planning ahead (so that, where possible, the appropriate seed source can be available when needed; see Chapter 100 FSH 2409.26f, known as 10-year seed procurement planning); and 2) keeping comprehensive records. Record-keeping should include not only the specific seed source (original geographic source, type of scale-up, nursery origin, and other pertinent information) but the rationale for decisions. These records will allow the accumulation of experience in making genetic matches, the review of which support improvements in decisions over time.

General guidelines

The guidelines for choosing genetically appropriate sources for revegetation projects are organized as two companion chapters. This chapter provides the rationale and general considerations, presented as a sequence of questions. The narrative refers to species-specific information, organized in tables, that is presented in Chapter 10. Chapter 9 presents a sequential set of considerations, and how they might influence the genetic source decision. Chapter 10 provides more information on additional resources to be consulted as one works through the questions. Then, Chapter 11 provides several case studies with some specific situations and species, providing examples of how to work through the guidelines first presented in this chapter, and using information from Chapter 10 to make informed choices.

The steps in the process to determine what source material is genetically most appropriate understandably consider both the nature of the site and the genetic patterns of the species. It is a process of making the best available match. Just as in other match-making activities, there are few hard rules that fit every situation. So the emphasis here is on understanding the rationale for making a good decision. Although this process is best based on science, it remains an art in terms of relying on the discretion and integrating ability of the project manager. The focus is on the species considerations, with some brief comments on site considerations at the end.

The guidelines have been organized to be applied individually for each species of interest. In situations where multiple species are being addressed for a project, the guidelines should be re-applied for each species as they each have their own suite of characteristics and conditions. In general, the guidelines take the form of a fairly linear decision key. There are nine steps in the key that involve species considerations and a tenth step involves site considerations. For any given species, every step is considered and then either deemed inapplicable (and thus, you proceed to the next point) or leads to further queries. The steps do not reflect priorities in consideration of information: they are all to be considered. Number 3 is also a possible endpoint, if it is determined that natural (unassisted) regeneration is adequate. Unlike the dichotomous keys used to identify plant species which trace a pathway that ultimately leads to one answer, this decision key provides information at each step, which in total will help inform the genetic source decision for a project (Figure 9.4).

Species considerations

1. Is a major goal of this project the maintenance of populations of native plant species to support natural levels of biodiversity and a healthy functioning ecosystem?

Yes.....Proceed to Number 3.

No......Proceed to Number 2.

2. Is the project isolated from other areas that have such a biodiversity or ecosystem health goal?

Yes.....Proceed at your discretion, maintaining the use of genetically appropriate materials as much as possible.

No......Proceed to Number 3.

3. Is natural regeneration of native species on (or formerly on) site likely to occur with sufficient success to render plant introductions unnecessary?

Yes.....Proceed with a natural regeneration management strategy. Sometimes doing nothing is the right or preferred management strategy. (Note: Mechanical treatments are outside the scope of this Guide, but obviously such treatments (including contour felling, erosion blankets, straw check-dams, wattles) should be considered where appropriate.)

No......Proceed to Number 4.

4. Is the species a state or federally listed (threatened, endangered, or candidate) species? (Refer to Box 12).

Yes.....If the species is not naturally rare, but is now a very geographically restricted species because of major habitat loss or other impacts, the specific nature of the situation and species will need to be considered. The guidelines offered here may not be the most appropriate approach, or may not be practical. There may be no or little opportunity for making new wild collections. However, seed collections may be available from a botanical garden. If the population has become very small, there may be demographic issues that supersede genetic considerations. And possibly, if much genetic diversity has been lost, or connectivity with other populations has been lost through fragmentation, there might be some advantage to the species to introduce seed material from other populations.

Because of the vulnerability of listed species, and the high risk of extinction, such species deserve individual attention and coordination with biologists and staff from other agencies to consider their biology, any genetic information, and the nature of the site. Such individual situations are beyond the scope of this guide. A general reference that provides information on both the theory and experience of reintroducing endangered plant species is 'Restoring Diversity: Strategies for Reintroduction of Endangered Plants' (Falk et al. 1996). In any event, consult with the US Fish & Wildlife Service regarding any federally listed plants, and check local laws regarding state listed plants. Proceed to Number 5.

No ......Proceed to Number 5.

5. Are there seed transfer rules in effect? (Refer to Table 10.1, Chapter 10)

Yes.....Proceed with using the information and guidance contained within the seed transfer rules for those particular species. However, not only is it unrealistic to expect that seed transfer rules can be continually and quickly updated to reflect new information, but they are necessarily generalizations. Any more recently available information, such as that presented here, can be mined to determine if there are caveats or other considerations that should be incorporated into local application of the seed transfer rules. Consideration can be given to the guidelines presented here and the tabular information in Chapter 10, in concert with the existing seed transfer rules. Take note of the geographic range and seed and pollen dispersal mechanisms. Proceed to Number 6.

No ......Take note of the geographic range and seed and pollen dispersal mechanisms. Proceed to Number 6.

6. Is the species facultatively clonal in a way that promotes resprouting after the disturbance experienced by the site? That is, will it reproduce by rhizomes, root suckering, bulbs, corms, or by sprouting from stumps or stems following fire or mechanical disturbance? (Refer to Table 10.2, Chapter 10).

Yes.....Many plant species have the ability to reproduce both sexually and asexually, and are not strictly one or the other. There is a fair degree of overlap between species that are clonal and those that are polyploids (Stebbins 1980). So polyploidy should be considered also if this is a possibility. Some native plant species in Region 2 that are facultatively clonal are presented in Table 10.2, Chapter 10. Refer to Box 13 for further discussion on clonal species and implications for planting. Proceed to Number 6a.

6a. Is the species dioecious?

Yes..... Ensure planting approximately equal numbers of males and females if introducing the species as plants rather than seeds. Proceed to Number 6b.

No...... Proceed to Number 6b.

6b. Is the species known to have some very (spatially) large clones?

Yes..... A conservative approach can be taken that involves sampling several to many clones and planting back more than the one pervasive clone, especially if clones are ancient. See rationale in Box 13. Proceed to Number 6.

No...... Sample and plant as for sexually reproducing species. Proceed to Number 7.

No ......Proceed to Number 7.

7. Is there evidence of genetic differentiation or local adaptation? (Refer to Table 10.3, Chapter 10).

Yes.....Consider how the genetic differentiation or local adaptation information (or potential for local genetic differentiation based on plant attributes) relates to the project scale and context. Although adaptation is the main interest, and genetic differentiation does not necessarily mean there are accompanying differences in adaptation, differentiation can be used as an indicator in the absence of direct studies on adaptation. That is, if one is interpreting information conservatively, and in the absence of direct studies on adaptation, one could assume that significant genetic differences within a species may reflect differences in adaptation that could affect planting success. Table 10.3, Chapter 10 provides a partial list of plant species native to Region 2 for which some genetic information is available. This list is neither comprehensive nor current (as new information is continually published). The table contains the type of information useful in making informed choices.

If information on local adaptation is available, the idea is to interpret this relative to the project site context. In some cases, quantitative information on local adaptation may be provided. For example, there may be studies that show local adaptation on the scale of meters or kilometers. So that is an indication of how finely-scaled the local adaptation, and hence the most appropriate genetic matching, could be. In other cases, the information on adaptation may not be quantitatively expressed, but related to some feature such as soil moisture, climate, soil type (for example, serpentine or pH level), or ecological community. The general range of the species that has been included in the genetic study is indicated, allowing one to determine the relevance of the information to the project site. For example, if there is a genetic study on a Utah population of a widespread species, this would have less relevance to a Region 2 project decision than one with samples from Colorado, Kansas, and Nebraska. As genetic diversity is not evenly distributed or necessarily similarly structured across the entire range of a species, studies that include samples closer to the project site or from conditions similar to the project site are more useful in making genetic decisions than otherwise.

In addition to adaptation of the species to local site conditions, there may be significant interactions between the local native plant species and other species, particularly pollinators and herbivores. So local differences in the pollen production timing, flower color, or leaf chemistry, for example, may have important consequences for other species. Check Table 10.3 for similar local adaptations that may affect other species. Such interactions between local populations and other species provide even stronger rationale for using local populations as source material, if possible, for revegetation. Proceed to Number 8.

No ......If the species of interest is not listed here, there still may be some information (recently) available so a quick check of the literature would be a good idea, if this is possible. Lack of evidence of local adaptation or genetic differentiation does not necessarily mean there is no genetic structure or local adaptation. Studies may not yet have been conducted. Alternatively, genetic measures may have been used that don’t well reflect adaptation. Assuming it is better to be conservative (that is, to err on the side of possible local adaptation) than not, one can then use proxies (a reasonable proxy is another related species in the same Genus) if there is no direct genetic information available. Check the table for other species in the same genus. These species may have similar characteristics, including a similar breeding system. However, this is not always the case so it is important to consider differences in breeding system, pollination systems, seed dispersal mechanism and other life-history traits that can have large effects on the spatial scale of genetic differentiation. As a reasonable proxy, in the absence of direct information (as discussed in Chapter 5), examine the species’ life-history traits for associations between traits and genetic structure and the scale of population differentiation (Tables 10.1 and 10.5, Chapter 10 and Table 5.4, Chapter 5). For example, if the species is outcrossing and wind-pollinated, a reasonable assumption (if there are no other contradicting traits or direct information) is that it may have little genetic differentiation among adjacent populations, allowing collections to be confidently made from other populations that are not too far removed from the site.

Remembering that dramatic environmental differences may be reflected in genetic differences of the plant species, some of which may be adaptive, major changes in soil type, elevation, soil moisture, or temperature can serve as clues for matching genetic source. For example, in the absence of other more specific information, for elevation transfers a distance of plus/minus 500 feet is used (FSH 1993). Experience has shown, at least for tree species, that moving sources too far up in elevation has more serious consequences (mortality, increased insect and disease problems, poor growth and form because of differences in phenology and snow loads) than moving too far down in elevation, which usually manifests itself as just a loss in growth (M.F. Mahalovich pers. com.). Proceed to Number 8.

8. Is the species a polyploid or does it have members or populations that are known to be polyploid?

Yes.....Does the species have variation in chromosome numbers that reflects variation in ploidy level among populations or individuals within the species (for example, are there both diploids and tetraploids in the species)?

Yes..... Proceed to Number 8a. Refer to Box 14 for some information on polyploidy that provides the rationale for these guidelines.

No...... Proceed to Number 9.

8a. Do you know which ploidy levels for this species were resident on the site prior to disturbance?

Yes..... Proceed to 8b.

No...... If possible, obtain a determination of ploidy level from genetic analysis (flow cytometry). This ploidy-determination service is available from laboratories such as NFGEL (USDA Forest Service, Placerville) and other research institutions. There is also a ploidy analyzer at the Rocky Mountain Research Station and the Seed Lab at Oregon State University, Corvallis, OR. Many universities also have cytology labs with flow cytometry capability. Once ploidy has been determined, then proceed as ‘yes’, above. If this is not known and cannot be determined, refer to Table 10.4, Chapter 10 for information on species in Region 2 with variable ploidy levels. Use the most common cytotype for the species (and in your geographic area, if that information is provided) if there is not more specific information on local (to your site) cytotypes or information that shows correlations between cytotypes and environment (adaptations) that may relate to your project site. Then proceed to Number 9.

8b. Was there on this site (or is there, on adjacent sites) more than one ploidy level (cytotype) for the species?

Yes..... If there were two or more cytotypes on the project area or adjacent areas, the goal is to avoid introducing new cytotypes, planting in the wrong ratio (if one is/was much more dominant), or creating novel (and probably less fit) hybrids between introduced and adjacent or resident cytotypes. Consulting Table 10.4, Chapter 10 for information on the species (or using the information you have on local cytotypes), plant back the same cytotypes, being particularly careful to maintain appropriate ratios among cytotypes if there was one dominant cytotype. Proceed to Number 8c.

No ...... If there is only one ploidy level (cytotype) for the project area and adjacent area, then plant this cytotype if possible. Proceed to Number 9.

8c. Are there known adaptations associated with any cytotypes? (Consult Table 10.4, Chapter 10).

Yes..... The information on what cytotypes are local and those with local adaptations should be consistent (that is, a decision between the two should not have to be made). But if the project area is very large and encompasses differences (for example, in elevation or soil type) for which there are adaptive differences among cytotypes, then this pattern can guide the installation of the cytotypes, and result in planting them in those areas for which they are known to be adapted. Proceed to Number 9.

No ...... Proceed to Number 9.

No ......Proceed to Number 9.

9. What is the main breeding system of the species? (Self compatible, self incompatible, monoecious, dioecious, gynodioecious, some cleistogamous, dichogamous, or heterostylous.) What is the mating system? (Outcrossing, selfing, or intermediate.)

As previously described, the breeding and mating systems have implications for both the continuing reproduction of the introduced plants, and the likelihood of their genes mixing with neighboring plants. Table 10.1, Chapter 10 provides some information on species' breeding systems. Table 10.5 provides information on mating systems and evidence for inbreeding or outbreeding depression in some native plant species of Region 2.

A few generalizations can be made about selecting plants for revegetation, based on their breeding and mating systems. First, dioecious plant species, if introduced as plants rather than seeds, should be introduced in approximately equal numbers of males and females. This will help conserve the genetic diversity and promote successful pollination. Second, species that are outcrossing and susceptible to inbreeding depression should be represented with considerable diversity—a wide sampling of individuals from suitable (within local adaptation bounds) populations. This will help guard against installing closely related family members that, when they cross, may produce seedlings that exhibit inbreeding depression. Third, if the species is a selfing plant, or shows high levels of inbreeding under normal conditions, then there may not be the need to be as concerned about the potential for inbreeding depression.

Site considerations.

Site context: It seems appropriate to use species information more conservatively (that is, try to match closely) when there are other values to protect, including the genetic integrity and ecosystem health of neighboring sites such as research areas or natural areas.

Site homogeneity: Some have suggested that introducing plants with a varied genetic background or higher levels of genetic diversity than locally available is a good strategy for revegetating heterogeneous sites. However, site heterogeneity can encompass many conditions, and either be natural or a result of some human disturbance. If site heterogeneity is natural—such as a steep gradient in elevation or moisture, a mixture of soil types, or some other natural condition—then consider first any information on genetic diversity or local adaptation based on similar sites.

For example, is there information in Table 10.5, Chapter 10 that indicates there may be local adaptation, at a fine spatial scale (consistent with that of the site)? If the site conditions are disturbed because of human influence, consider first whether some site modification is required, or a different species should be used. If the site conditions are novel or unusual, they may be outside the range of adaptation of the local species. Other species may be useful in reconditioning the site, and perhaps appropriate populations of native species could be reintroduced later. Consult Boxes 11 and 12.

Successional stage: It may be appropriate to start the revegetation effort at an earlier seral stage than the one present prior to the disturbance. For example, if site conditions have deteriorated significantly, such as complete removal of the A horizon, then using an early-seral stage species may be more appropriate than jumping to the pre-disturbance mid- to late-seral species. This discussion is beyond the scope of this Guide. Some general references on the topic include Kitchen and McArthur 2001, Brown and Amacher 1999, Wade and Thompson 1999, Jones 1997, Wade and Tritton 1997, and Tritton and Wade 1996.

Figure 9.1. Forest Service Seed Collection Zones for the State of Colorado.

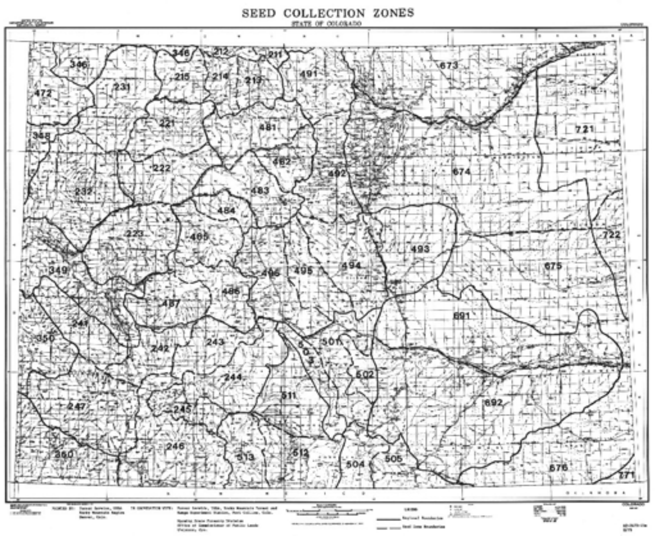


Figure 9.2. Forest Service Seed Collection Zones for the State of South Dakota.

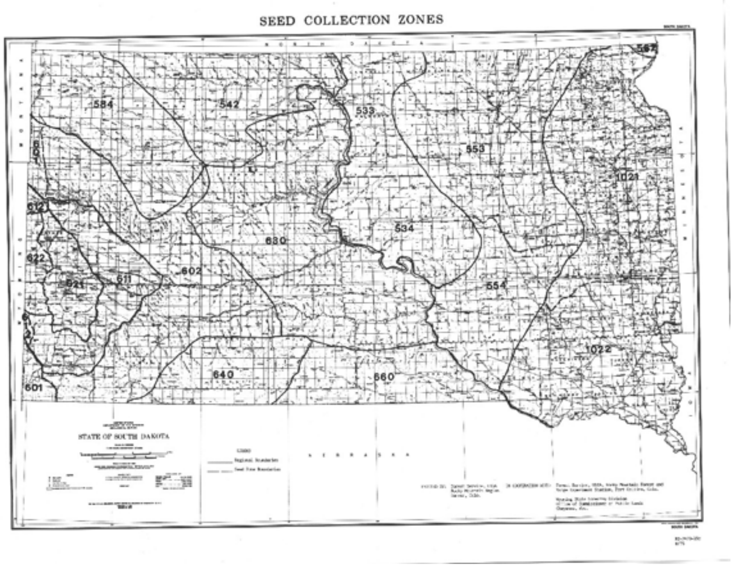
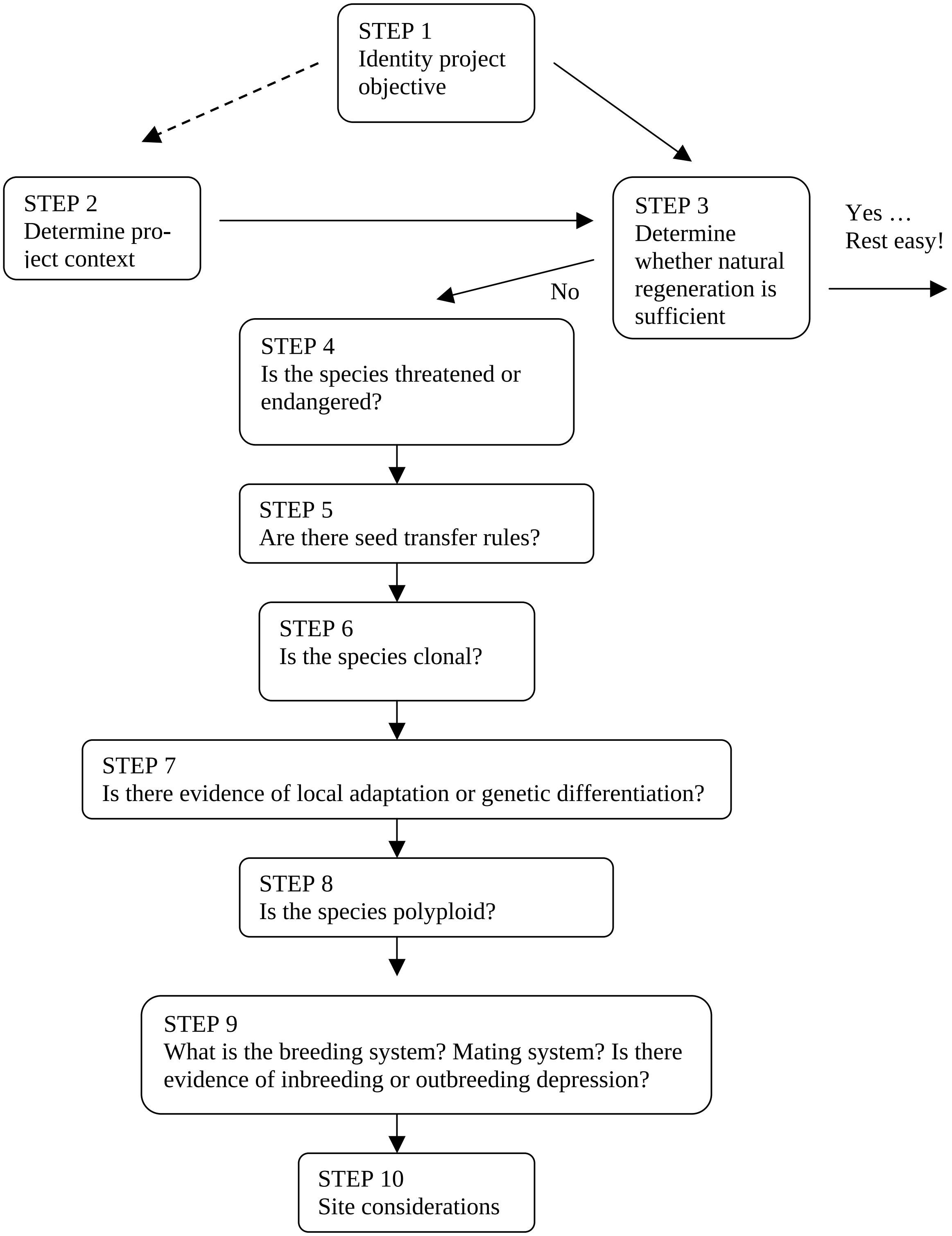


Figure 9.3. Forest Service Seed Collection Zones for the State of Wyoming.

Figure 9.4: Basic steps for informing choices on genetically appropriate source for each species involved in a revegetation project. Although the project objectives and context could conceivably reduce the need to consider genetic issues (and hence, dotted lines), it may be well-advised to include genetic considerations in any event, if possible. See text for description of the steps presented here.



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Box 12: Native Plant Species in FS Region 2 that are Listed (or Candidates for Listing) under the Federal or a State Endangered Species Act[1]

The federal or state protected status of a species is dynamic: new species are added to the list through a petition process, and currently listed species may move off the list as their status improves. Consequently, the list below may not reflect the current status of all native plant species in Region 2. At the time this Guide was published, 25 plant species were protected under the federal ESA in Region 2, either with the full protections of endangered or threatened status, or provisionally as candidates for such protection.

In addition to federal or state listing, the Forest Service maintains a list of sensitive plants. As of December 1, 2003, there were over 80 plant species on this list for Region 2 (USDA Forest Service 2003). Any species that are on the candidates list for federal listing are automatically considered sensitive species for the Forest Service. Other conditions that can prompt a designation of sensitive in Region 2 include a restricted distribution, vulnerable habitat conditions, low dispersal ability, or downward trend in population size. This list is more dynamic in composition that federal or state lists.

The only state within Region 2 with its own Endangered Species Act is Nebraska. In Nebraska, in addition to State listing of four of the plant species on the federal list, there are three additional plant species listed at the State level.

Table B12.1. Native plant species in FS Region 2 that are listed (or Candidates for Listing) under the Federal or a State Endangered Species Act.

			Status[2]	
Scientific name	**Common name**	**Historic range (by state)**	**Federal**	**State[3]**
Asclepias meadii	Mead’s milkweed	IA, IL, IN, KS, MO,WI	T	
Astragalus humillimus	Mancos milk-vetch	CO, NM (no known current occurrences in CO)	E	
Astragalus tortipes	Sleeping-Ute mild-vetch	CO	C	
Astragalus osterhoutii	Osterhout milk-vetch	CO	E	
Botrychiun lineare	Slender moon wort	CO, MT, OR, WA	C	
Cypripedium candidum	Small white lady’s slipper	NE		T
Eriogonum pelinophilum	Clay-loving wild buckwheat	CO	E	
Eutrema penlandii	Penland alpine fen mustard	CO	T	
Gaura neomexicana var. *coloradensis*	Colorado butterfly plant	CO, NE, WY	T	E
Lesquerella congesta	Dudley Bluffs bladderpod	CO	T	
Panax quinquefolium	Ginseng			T
Pediocactus knowltonii	Knowlton cactus	CO, NM	E	

Table B12.1. Continued.

			Status[2]	
Scientific name	**Common name**	**Historic range (by state)**	**Federal**	**State[3]**
Penstemon debilis	Parachute beard tongue	CO	C	
P. grahamii	Graham beard tongue	CO, UT	C	
P. haydenii	Blowout penstemon	NE, WY	E	E
P. penlandii	Penland beardtongue	CO	E	
P. scariosus albifluvis	White River beardtongue	CO, UT	C	
Phacelia submutica	DeBeque phacelia	CO	C	
P. formosula	North Park phacelia	CO	E	
Physaria obcordata	Dudley Bluffs twinpod	CO	T	
Platanthera leucophaea	Eastern prairie fringed orchid	AR, IA, IL, IN, ME, MI, MO, NE, NJ, NY, OH, OK, PA, VA, WI	T	
P. praeclara	Western prairie fringed orchid	IA, KS, MN, MO, ND, NE, OK, SD	T	T
Salicornia rubra	Saltwort			E
Sclerocactus glaucus	Uinta Basin hookless cactus	CO, UT	T	
S. mesae-verdae	Mesa Verde cactus	CO, NM	T	
Spiranthes diluvialis	Ute ladies' tresses	CO, IX, MT, NE, NV, UT	T	T
Trifolium stoloniferum	Running buffalo clover	AR, IL, IN,KS, KY, MO, OH, WV	E	
Yermo xanthocephalus	Desert yellowhead	WY	T	

[1] Source of information on federal listings: US Fish and Wildlife Service (http://www.fws.gov).

[2] E Endangered, T Threatened, C Candidate species (Candidate species: The species is being considered for listing. The Fish and Wildlife Service has sufficient information to propose listing the species as threatened or endangered, but has not yet taken action.)

[3] Nebraska only (within Region 2). Source of information for these state-listed plants: http://www.ngpc.state.ne.us

Literature

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Box 13: Genetic Considerations in Restoring Clonal Species

Although there are various types of vegetative growth—including repair or regeneration of injured plant tissue—focus here is on reproductive growth, where there is duplication of an individual genotype. The terms "vegetative reproduction" will be used here interchangeably with "vegetative growth" or "clonal growth". A clone is a genetic individual and members (or copies) of a clone are called 'ramets' when propagated for planting purposes. Among higher plant species, clonal growth is much more common in angiosperms than in gymnosperms, and, within the former, more common in monocots than in dicots (Tiffney and Niklas 1985). Rather than being strictly clonal, plant species are often facultatively clonal: they may be more or less sexual depending on the particular population (for example, peripheral populations of a species tend to have more asexual reproduction than other more central populations, where mates are more abundant), site conditions, or the year. For example, sexually reproducing tree species such as white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) B.S.P.) particularly make use of vegetative reproduction near their northern distribution limit (Légère and Payette 1981).

Much has been written on the population biology and ecological and evolutionary significance of clonality (see, for example, Jackson et al. 1985). But those topics are beyond the intent of this box. Here, the focus is on the genetic aspects of clones that are particularly relevant to revegetation projects.

Genetic diversity, and its maintenance, is still very important even if a species can reproduce vegetatively

Genetic diversity confers the same attributes and advantages (such as ability to adapt to changing environmental conditions) to species that can reproduce vegetatively as to those that don't. In a survey of 21 clonal plant species with a wide range of life histories, Ellstrand and Roose (1987) found intermediate (in the range of genetic diversity for plant species) levels of genetic diversity. There does not appear to be any evidence to suggest that the ability to reproduce asexually is associated with lower levels of genetic diversity.

Plant species with the capacity for clonal growth may have more genetic distinctiveness among populations than sexually reproducing species

This is a broad generalization, but well founded in logic. Genes don't travel as far when restricted to vegetative growth (rhizomes, branches breaking off and rooting, and so on) as when traveling with the wind through pollen or seeds. Consequently, vegetative growth would tend to keep genes more localized. Ellstrand and Roose (1987) found, among the clonal species they reviewed, that most clones were restricted to one or few populations (that is, there were few widespread clones). Even if the species also reproduce sexually to some extent, overall there could be less gene flow than if there was no asexual reproduction.

Individual clones might occupy large geographic areas

If a species has the ability, at least, to reproduce asexually, then that feature should be considered when sampling for and introducing new plants. If the population has reproduced asexually to a large degree, then it is possible that particular clones have developed very large distributions This has been shown to be the case for some areas of aspen (*Populus tremuloides* Michx.). A single aspen clone has been identified in Utah, for example, that covers over 106 acres, and other clones in the same area were estimated at 25 acres to over 200 acres (Kemperman and Barnes 1976). The decision then becomes whether to install a similar clonal structure to the pre-disturbance structure (for example, using just a few clones, planted in multiple copies) or to use more genetic diversity and allow natural selection to determine which clones become more spatially pervasive. In long-lived species, disturbances (such as fire) may represent opportunities to replace old and pervasive clones that may be better adapted to the past than well suited for future conditions. The natural recruitment of aspen seedlings after a fire has been considered such an opportunity for genetic renewal in regions where there are large, old clones (Tuskan et al. 1996, Stevens et al. 1999). In addition, if the species is dioecious, it makes sense to include approximately equal numbers of male and female clones in the mix.

Clonal growth does not necessarily result in large pervasive clones

However, in many cases, the ability to reproduce asexually does not result in large clones, or dampen the amount of genetic diversity in populations (as would be expected if just a few clones were dominant). A study of seven populations of the clonal plant *Carex scopulorum* var. *scopulorum* in the Rocky Mountain National Park did not reveal any large, pervasive clones. Sixty percent of the samples (tillers) were genetically different (Linhart and Gehring 2004). In the Ellstrand and Roose (1987) study, clone size of big bluestem (*Andropogon gerardii* Vitman) from the Konza Prairie Biological Station, Kansas averaged about 2 meters in diameter and areas of prairie of 100 m² were calculated to contain an average of approximately 32 clones (Keeler et al. 2002). These examples illustrate that clonal growth does not necessarily result in large pervasive clones. Rather, it can mean that individual genotypes are kept in the population for long periods of time and the population maintains the ability to reproduce even in years that aren't conducive to sexual reproduction. In the absence of direct information to the contrary, it may be a lower risk to plant seedlings or only a small number of ramets per clone—within whatever bounds are determined by local adaptation—and let natural selection determine which clones become more pervasive, rather than planting larger numbers of ramets per clone.

Plants that appear to be members of clone may in fact be different individuals

If a plant species is known to be capable of vegetative reproduction, then clumps, clusters, or closely situated plants might be immediately assumed to be members of the same clone. However, that is not always the case. In some cases, 'apparent' clone identity has been refuted by genetic analysis. For example, two dioecious tree species that are native to the mid-western US, Osage orange (*Maclura pomifera* (Raf.) Schneid) and *Gleditsia triacanthos*, both typically grow in tight clumps—a group of two or more stems that are touching at their bases. The ability of both species to resprout multiple stems after injury had led to the speculation that many clumps might be single individuals. However, genetic analysis revealed that in both cases the great majority of clumps contained more than one individual and, in many clumps, all the stems were genetically unique (Schnabel et al 1991). Similarly, tightly grouped stems of whitebark pine (*Pinus albicaulis* Engelm.) were found to be close relatives rather than clonal members (Rogers et al. 1999) and circular arrangements of coast redwood (*Sequoia sempervirens* D. Don) that had been presumed to be clonal (a so-called 'fairy ring' that presumably sprouted from the perimeter of large, pre-existing trees) were found to almost always contain more than one clone (Rogers 2002).

The lack of correspondence between the spatial arrangements of clonal plants and their real genetic identity makes identification of unique individuals difficult. This problem of distinguishing between members of a clone and different clones has been cited for many plant species including a creosote bush (*Larrea tridentata*) (Ebert and McMaster 1981). One implication is that if it is desirable to do single-genotype seed (or cutting) collections, collections should be kept separate for every plant unless it is absolutely certain that two plants represent the same clone.

Literature

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Box 14: Polyploidy in Native Plant Species: Implications for Revegetation Projects

Polyploidy is an important consideration in revegetation projects because polyploid species are common. Among angiosperm species, the estimates for the proportion of species that are polyploid range from 30% to 52% (Stebbins 1950, Grant 1981). Many of the commonly used restoration grass species are polyploids (for example, big bluestem (*Andropogon gerardii* Vitman) and blue grama (*Bouteloua gracilis ((*Willd. ex Kunth) Lag. ex Griffiths). Use of the term “polyploid species” here refers to a species in which many, if not all, of its members have more than two sets of chromosomes. There may be some species where polyploid individuals occasionally arise (such as *Populus tremuloides*), but the focus here is only on species where polyploidy is a well-established feature of the species. Polyploids are far less common in gymnosperms: coast redwood (*Sequoia sempervirens* D. Don) is one rare exception. It is a hexaploid.

This is not a comprehensive review of polyploidy: its origin, relationship with speciation, inheritance, and so on. The intent is to provide some general characteristics of polyploids and genetic considerations that are pertinent to their use in revegetation projects.

The main concern with translocation of polyploids involves species that have various levels of ploidy within them—for example, species with both diploid and tetraploid individuals. Sometimes these mixed-ploidy species have populations that are exclusively one type or another, and sometimes various ploidy levels or cytotypes are mixed within populations. There are two major implications of polyploidy for making genetically appropriate decisions for revegetation projects. First, different ploidy levels may be sexually incompatible, making it desirable to have sufficient numbers of the same ploidy level to allow sexual reproduction. For example, there is an incompatibility that prevents most pollen tubes of tetraploid plants from reaching ovules within in diploid plants of fireweed (*Chamerion angustifolium* (L.) Holub) (Husband et al. 2002). Second, in some species, mating between cytotypes can produce less fit or sterile progeny (one of the mechanisms of intrinsic outbreeding depression mentioned in Chapter 5). This is also illustrated by crosses between diploid and tetraploid cytotypes of fireweed. The resulting triploid progeny, when they do form, are only 9% as fertile as diploids (Burton and Husband 2000). Third, different ploidy levels may have different types of adaptations with or without the presence of mating incompatibilities. This might be expected, in particular, for those polyploid species that have different ploidy levels in different populations, rather than mixtures. The distribution of fireweed cytotypes in North America suggests there are adaptive differences between major cytotypes. Most populations contain a single cytotype, with diploids growing at higher latitudes and altitudes than tetraploids. A zone of contact occurs across North America from the southern end of the boreal forest, south along the Rocky Mountains (Burton and Husband 2000). All three cytotypes occur in the contact zone, but triploids occur at low frequency because of the incompatibilities noted above.

Some species have a different kind of polyploidy and exhibit a large range of cytotypes. These sometimes occur in mixed populations with no obvious, undesirable effects. Often, however, undesirable effects may be balanced by other selective benefits and differences in adaptation. For example, in a comparison of various measures of photosynthesis in plants of five different ploidy levels of shadscale saltbush (*Atriplex confertifolia* (Torr. & Frém.) S. Wats.) (from (2x) diploids to (10x) decaploids, where x refers to the base number of chromosomes), it was determined that the cytotypes differed significantly. Average photosynthetic rates per unit leaf area were lowest in the diploid, similar in 4x, 6x, and 8x, and highest in the decaploid (Warner and Edwards 1989). Different individuals in a single population of big bluestem can also have varying number of copies of the base number of chromosomes, represented by x=10, up to 9x. When an individual with a new multiple chromosome number arises in a population, it has a mating disadvantage that needs to be counterbalanced by some other selection benefit, such as larger size and more flowers (Keeler and Davis 1999). Some of the cytotypes, however, cross freely and form progeny of varying chromosome numbers (Norrmann et al. 1997).

Switchgrass (*Panicum virgatum* L.) also has an impressive polyploid series from 2x=18 to 12x = 108. When populations have mixtures of cytotypes, primarily tetraploids and octoploids occur and there is a geographic pattern to the frequency of the different common cytotypes. Martínez-Reyna, and Vogel (2002) found that mating between tetraploids and octoploids results in a high proportion of inviable seeds which was worse when the tetraploid served as the mother, explaining the rarity of hexaploids in the mixed populations. In addition, this species has distinct upland and lowland cytotypes that tend to be genetically and morphologically distinct. Casler and others (2004) showed that cytotype and complex correlations with habitat explained most of the variation in crossing success among cytotypes and populations from different latitudes.

The subgenus *Tridentate* of *Artemisia* is a polyploid complex (x=9), composed of 11 species with ploidy levels from 2 x to 8x but mainly 2x (diploids) and 4x (tetraploids). The principal species in this complex is Big sagebrush (*Artemisia tridentate* Nutt.) which has several subspecies in Region 2. Considerable research has been conducted on the systematic relationships of taxa in this complex, the nature of their hybrids, and evidence of local adaptation. One study of the *A.t.* subspecies revealed that the diploid plants are larger than the tetraploids—the latter being adapted to drier conditions, perhaps as a result of their slower growth rates (McArthur et al. 1998, McArthur and Sanderson 1999, Vallés and McArthur 2001).

Some species from Region 2 that are known to have variable ploidy levels are listed in Table 10.4. In general, the goal is to reintroduce individuals with the same ploidy levels as the pre-existing or neighboring plant populations of this species. If there is more than one ploidy level, roughly the same ratio of cytotypes should be introduced: that is, if there is a predominant type, it should be the predominant type for the introduced plants. If polyploidy is known to be a feature of the species, but the ploidy level of the resident (or neighboring) population(s) is unknown, a determination of ploidy level can be obtained from genetic analysis. (Such services are available from NFGEL, USDA, Placerville, CA and other research institutions with flow cytometry capability).

There are other, more complicated, issues here that have been avoided for simplicity. For example, there is an important distinction between the chromosome complement of a polyploid species (referred to as the ploidy level) and the genetic system (for example, a tetraploid could have tetrasomic or disomic inheritance). The latter characteristic refers to how the chromosomes are inherited (and how the polyploid originated, from hybridization between different species or subspecies followed by chromosome doubling in contrast to simple chromosome doubling), and thus has consequences for the genetic diversity of the species and crossing compatibilities. So, for example, some polyploids may resemble diploids in their genetic systems. For many species, the type of inheritance may not be known and the interpretation and implications for genetic source is complicated and uncertain.

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Chapter 10

Information on Region 2 Native Plants

The use of this practical guide to assist in making choices about sources of native plants for revegetation requires close attention to the ecology and genetics of targeted plant species. Although not every species of interest has been studied ecologically and genetically, many have been examined, and there are thousands of publications and documents containing information useful to the decision process.

In this chapter, Tables 10.1–10.5 contain information on flower and cone-bearing plants (angiosperms and gymnosperms) that is useful for making informed decisions about the most appropriate sources of plant materials. The tables should be consulted while navigating a species through Chapter 9, as will be illustrated in Chapter 11. But, not all species or genera of interest will be represented in all or perhaps any of the tables. The tables concentrate on herbaceous species for several reasons. First, they are not included in the Seed Handbook (FSH 2409.26f) for Region 2. Second, as a group, they are more genetically structured and variable than trees (especially compared to conifers with their wind-dispersed pollen and many flowering trees such as oaks and willows with wind-dispersed pollen or seed) over an equivalent spatial scale. Third, they have a wide-range of mating systems and gene dispersal capabilities that differ from the average wind-pollinated coniferous tree. Some woody plants are presented for comparison. Although woody plants are included in the FSH, their biology is quite variable, and knowledge about them may help encourage appropriate use. Only a few pertinent papers have been presented for most of the tabulated trees.

The focus here is on ecological genetic information. Information, particularly that derived from genetic studies, is not available for all plant species in the region. It is assumed that a general knowledge about the habitat affinities and elevational boundaries is already known, or easily accessible. Furthermore, it is beyond the scope of this Guide to comprehensively cover all available information for the hundreds of species in the region. A sample of species was selected that is widely considered for revegetation. This list was augmented with species that have research findings useful for illustrating the concepts important to making appropriate genetic decisions. The species studied by researchers are often community dominants, common species that colonize newly opened sites, rare species that are protected under the federal or a state endangered species act, or species with noticeable traits that appear to have adaptive value.

In Chapter 11, a sample of species from Tables 10.1–10.5 will be run through the logical series of questions provided in Chapter 9. These tables have been constructed to highlight the most important information available for making wise genetic decisions. We expect that from time to time, more detailed information will become available for important restoration species. To show how these questions can be used with more detailed information as it becomes available in other formats, we will also run through an example of a species that has more detailed information available. Such information can help to refine or reinforce previous decisions.

Tables 10.6-10.8 serve as examples with added information. Each of these added tables contains information on a well-studied species, and the species used have contrasting life-history attributes. These tables provide a larger variety of information pertinent to genetic decisions than could be fit squarely into the Table 10.1–10.5 format. The intent is to illustrate that the information in Tables 10.1–10.5, though the *most* important, is not *all* of the information pertinent to making careful decisions. Additional information can and should be incorporated as it becomes available to help refine decisions made by navigating the steps in Chapter 9.

Description of data tables provided in this chapter

Table 10.1. General species life-history and breeding system information for a sample of species from Region 2. Many, but not all of these species have some genetic information available. To be found in subsequent tables, we will have found information on vegetative reproduction (Table 10.2), adaptation or genetic differentiation (Table 10.3), variable cytotypes (Table 10.4), or inbreeding or outbreeding depression (Table 10.5). Some important results from genetic studies of species that did not have information available for Tables 10.2–10.5 are noted in the comments column of Table 10.1. For example, if mating system, inheritance of traits, or gene flow by pollen dispersal have been studied in a single population of a species, the results may be mentioned in this table. Such data can provide some insight into predicting the potential for population differentiation, inbreeding depression, or outbreeding depression. The columns labeled “Types of genetic studies” and “References” list useful studies for each species and give an indication of how well studied the species is (in terms of ecological genetics). Most species in the plant materials Chapter 8, Table 8.2 have also been included in this table.

Table 10.2. Characteristics of some Region 2 native plant species that are known to reproduce vegetatively or resprout after disturbance. FEIS (2004) was the source of information for many species on type of growth structures and propensity for vegetative growth. If a species is known to form clones, available information on clone size and genetic diversity is noted.

Table 10.3. Information on local adaptation or genetic differentiation in some plant species native to Region 2. Some of the information on local adaptation or morphological differentiation comes from reciprocal transplant and common garden (or other common environment) studies. Often, there is information included on population differentiation based on molecular marker variation. Examples are also provided on the disruption of species interactions or if there are data on geographic patterns of variation in morphology, physiology, species interactions, or other important variables that can play a role in translocation effects. Consult Chapters 4 and 5 for help on interpreting genetic diversity information, especially abbreviations of diversity parameters.

Table 10.4. Region 2 native plant species that have variable ploidy levels (cytotypes). This table includes species known to exhibit variable ploidy levels (cytotypes). Information on differ-

ences in adaptation among cytotypes, mating incompatibilities, and morphological differences are noted.

Table 10.5. Species from Region 2 studied for inbreeding or outbreeding effects. As explained in Chapter 5, inbreeding depression is sometimes detected as an increase in fitness (heterosis) upon mating of nearby populations that have experienced some genetic erosion but show no evidence of inbreeding depression within populations. For this reason, within or between population inbreeding depression is indicated (w versus b). It is important to realize that not all phenotypic traits are tied to fitness. Some studies may find heterosis in a trait that is of importance for marketing of germplasm for a specific purpose but has nothing to do with survival or reproduction. To be relevant to inbreeding or outbreeding depression, the trait measured needs to be fitness-related and preferably a component of fitness (Chapter 5). Many studies of outbreeding depression have been done on a small spatial scale (Chapter 5). These can sometimes point to the presence of adaptive differences over a small spatial scale. The larger spatial scale studies and those that involve crosses among subspecific taxa are the most relevant for guiding decisions about translocation to different areas within a species range. The spatial scale of cited experiments is indicated.

Tables 10.6–10.8. Examples of detailed ecological genetics tables for a set of three species with contrasting life-forms and reproductive biology. These tables will be used to illustrate the use of additional information when it becomes available. The new information can be addressed with the steps outlined in Chapter 9. The tables also illustrate how additional data from outside Tables 10.1–10.5 might refine or corroborate a previous decision.

Table 10.1. General species life-history information for a sample of species from Region 2 that have some genetic information available. Most names are included in at least one additional Table (10.2-10.5, Table 8.2). Taxonomy follows USDA PLANTS database as of September 2004 (USDA NRCS 2004, http://plants.usda.gov/index.html). Commonly used synonyms are provided. Abbreviations for column contents are in the table footnote. Apomictic seed production in this table is by agamospermy. See FEIS database for elevations, habitat affinities, and general ecology.

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Grasses:											
Achnatherum hymenoides (Roemer & J.A. Schultes) Barkworth (=*Oryzopsis hymenoides* (Roemer & J.A. Schultes) Ricker ex Piper; *Stipa hymenoides* Roemer & J.A. Schultes)	Indian ricegrass	Poaceae	P	WR: NE, KS, and WI w. to WA and CA, and in west from Canada to MEX on drier sites below 1000 m	W (A, G, V)	W	SC/P,CL	seed dormancy and seed shattering, hybridization, breeding system	Jones 1990, Jones et al. 2004	Natural genetic variation in seed shattering and seed dormancy selected against in production of cultivars. Hybridizes with several species of *Stipa* (*Nassella*) (Johnson & Roglar 1943, Johnson 1963, Jones 1999), but most hybrids are sterile.	—
Andropogon gerardii Vitman	Big bluestem	Poaceae	P	G: Saskatchewan east to ME, south to AZ and FL	W	W	SI/P	Clonal, variable cytotypes, seed source and competition, seed source and mycorrhizae	Gustafson et al. 1999, Schultz et al. 2001, Keeler et al. 2002, Gustafson et al. 2004a,b	Significant functional differences among seed sources. Local adaptation to mycorrhizae.	—
Bouteloua curtipendula (Michx.) Torr. Two varieties: 1) *B. c.* var. *curtipendula* 2) *B. c.* var. *caespitosa* Gould & Kapadia	Sideoats grama	Poaceae	P	1) G: Canada s. to Mexico, OR and WA to Atlantic coast (absent from CA and NC; 2) G: CA east to CO, south to Mexico and TX	W	W	—/P	Common garden, molecular markers	Olmstead 1945	Fankel & Galun report some forms apomictic (agamospermous), and plants highly outcrossing.	—
Bouteloua gracilis (Willd. Ex Kunth) Lag. ex Griffiths	Blue grama	Poaceae	P	G: BC east to Manitoba; all w. states except OR and WA, s. to central MEX, east to TX, OK, IL, MI, NY, MA, CN, MN; disjunct in SC	W, V, I	W	—/P	Cytological, common garden (see Table 10.8)	Riegel 1940, McGinnies et al. 1988, Baskin & Baskin 1998) Wooley et al. 1991, Phan et al. 2003, Fu et al. 2004	Fankel & Galun (1977) report some forms apomictic. Larval food plant of Federally Threatened Pawnee mountain skipper (Wooley et al. 1991). Reported to be outcrossing to unspecified mating system (Fryxell 1957).	MFM in prep.

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Bromus carinatus Hook. & Arn.	California brome	Poaceae	A, B, P	WR: WA, OR, CA	G	W	SC/P	Distribution and determination of cleistogamy, cytology and hybridization	Harlan 1945a,b, Stebbins & Tobgy 1944	Sometimes lumped with *B. marginatus* (FEIS).	—
Bromus marginatus Nees ex Steud.	Mountain brome	Poaceae	P	G: AK south to CA, east to NM, CO, NE, SD; disjunct in MA, NY, IL	G, V?	W	SC/P	.	.	Sometimes lumped with *B. carinatus* (FEIS).	—
Buchloe dactyloides (Nutt.) Engelm	Buffalograss	Poaceae	P	G: In Canada, in s. Sask. and Manitoba; in US: MT, WY, NV, UT, AZ east to WI, IL, MO, AR. Also in GA and northern MEX; incidental in VI	V & G	W	SC/most D, sometimes M or P	Distribution of sex ratio of flowers, ploidy, and RAPD variation in sourthern populations	Huff & Wu 1992, Huff et al. 1993, Johnson et al. 1998, FEIS	Ungulates ingest and disperse viable seeds (Ortmann et al. 1998). Burs can cling briefly to animals and aid in seed dispersal. Sex determination is highly heritable (Huff & Wu 1992). Monoecoius forms tended to be < 25% of stems and tended to be in peripheral populations.	—
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes (Synonyms in PLANTS: 1) *D. s.* var. *spicata* 2) *D. s.* var. *pinetorum* Piper 3) *D. s.* var. *longipila* Scribn. & Merr.)	Oatgrass, poverty grass	Poaceae	P	G: Ak and continental US except CA, NV, UT, AZ and NE; 1) G: Newfoundland to BC and south to FL, KS, NM, and to OR and ID in far west. 2) R: n. central and central CO, 5300-8100 ft also in New Zealand	V & G	W	SC/P,CL	flower sexual system, progeny performance, inbreeding effects, phenotypic plasticity and genetic drift	Clay & Antonovics 1982, 1985, Clay 1983, Scheiner & Teeri 1986	Progeny from cleistogamous flowers less fit than those from open flowers. In New Zealand, some apomixis in addition to cleistogamy (Philipson 1985).	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Deschampsia caespitosa (L.) Beauv	Tufted hairgrass	Poaceae	P	G: AK to Greenland, in western US, south to northern Mex (not in NE to OH or south to TX and FL). Also in southern Australia.		W	SI/P	Allozyme studies of genetic diversity, gene flow, environmental gradients in flowering and resource allocation (Australia)	Hodgkinson & Quinn 1978, Quinn & Hodgkinson 1984, Gehring & Linhart 1992; Purdy & Bayer 1995	The South Dakota Natural Heritage Program has listed tufted hairgrass as rare in South Dakota. Facultative apomixis (Fryxell 1957).	—
Elymus canadensis L.	Canada wild rye	Poaceae	P	G: Canada south to CA and TX, east to MN and SC (absent from LA to GA and FL)	G	W	SC/P	.	.	Barkworth & Dewey (1985) report most *Elymus* species are allopolyploids, have short anthers, and tend to self-pollinate. Hybridize with other species of *Elymus.*	—
Elymus cinereus (Scribn. & Merr.) A. Löve	Basin wildrye	Poaceae	P	G: western N. Amer. From CA to NM, CO, NE, MN	G	W	SC/P			.	—
Elymus elymoides (Raf.) Swezey ssp. *elymoides* (=*Sitanion hystrix* (Nutt.) J.G. Sm.); four subsp.; 1) *E. e.* ssp. *elymoides* 2) *E. e.* ssp. *hordeoides* (Suksdorf) Barkworth 3) *E. e.* ssp. *brevifolius* (J.G. Sm.) Barkworth, comb. nov. ined. 4) *E. e.* ssp. *californicus* (J.G. Sm.) Barkworth, comb. nov. ined.	Bottlebrush squirreltail	Poaceae	P	1) G: WA s. to s. CA, e. to AZ, MO, OH, ND, SD, NE; 2) WA, OR, CA, NV, ID; 3) OR s. to s. CA, e. to ID, MT, SD, and s. to TX; 4) WA, OR, CA, NV, ID, MT, WY, UT	G	W	SC/P	Common garden, genetic diversity among taxa, variation in seed germination	Clary 1975, Jensen et al. 1999, Jones et al. 2003, Young et al. 2003	A highly variable, short-lived perennial that naturally hybridizes with species of *Leymus,* often producing sterile hybrids. Outcrossing in *Elymus* species tends to be very low. Accessions from test plots varied among populations in seed germination response to cold temperatures (Young et al. 2003).	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Elymus glaucus Buckl. First two subspecies in R2: 1) *E. g.* ssp. *glaucus* 2) *E. g.* ssp. *jepsonii* (Burtt-Davy) Gould 3) *E. g.* ssp. *virescens* (Piper) Gould	Blue wildrye	Poaceae	P	1) G: western N. Amer. from AK to Mex, east to IN, IA; 2) CA, ID, MT, NV, OR, WA, WY; 3) AK to BC, WA to CA	G	W	SC/P	Common gardens, population structure, genetic diversity, hybridization among populations	Snyder 1950; Knapp & Rice 1996; Wilson et al. 2001; Erickson et al. 2004	Studies of allozyme variation indicate plants are highly selfing and that gene flow among populations is low (Knapp & Rice 1996, Wilson et al. 200). Evidence also points to some outcrossing within populations. Flowers disperse pollen from exerted anthers, plants commonly hybridize with *Sitanion jubatum* in nature (Snyder 1950), and wild-collected families of seeds segregate for a pubescence trait (Erickson et al. 2004).	—
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould 1) *E. l.* ssp. *lanceolatus* 2) *E. l.* ssp. *psammophilus* (Gillett & Senn) A. Löve	Streambank wheatgrass	Poaceae	P	1) WR: BC, Sask., Canada; Pacific coast states east to ND, SD, NE; and WI, MI, IL 2) WI, MI	G	W		Hybridization	Jones et al. 1995	Cytogenetics work on F1 hybrids with Snake River wheatgrass (*E. wawawaiensis* J. Carlson & Barkworth) examined nature of hybrid male sterility (Jones et al. 1995). Evidence for genomic incompatibilities causing male sterility in hybrids. Populations occur from sea level to 3,500 m. Thick, sod-forming growth allows to compete with invasive species once it is established (FEIS).	—
Festuca arizonica Vasey	Arizona fescue	Poaceae	P	G: NV, AZ, UT, CO, NM, TX	G	W		Population structure, diversity and influence of symbiotic fungi	Prendergast et al. (2004, web site), An et al. 1992	Much research on association with symbiotic fungi (for example, An et al. 1992).	—
Festuca thurberi Vasey in Rothr.	Thurber fescue	Poaceae	P	WR: WY, CO, UT, AZ, NM	G	W		Population structure	Prendergast et al. (Bingham web site- 2004)		—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Hesperostipa comata (Trin. & Rupr.) Barkworth (=*Stipa comata* Trin. & Rupr.) Two subsp. 1) *H. c.* ssp. *comata* 2) *H. c.* ssp. *intermedia* (Scribn. & Tweedy) Barkworth	1) needle and thread 2) intermediate needle and thread	Poaceae	P	1) G: Western US WA to CA, e. to TX, OK, KS, IA, NY 2) G: WA to CA, e. to TX CO, WY, MT	W	W	.	.	.	.	—
Koeleria macrantha (Ledeb.) J. A. Schultes (= *K. cristata* auct. p.p. non Pers., *K. gracilis* Pers., *Koeleria nitida* Nutt.)	Prairie junegrass, crested hairgrass	Poaceae	P	G: N. Amer. and Eruasia. Alaska to BC, east to Sask., Canada, south to CA, TX and LA, and into Mex. In most states, except s.e.	W, G	W	SI/P	common gardens, systematics, cytology	Robertson & Ward 1970, Arnow 1994, Monsen et al. 2004 v2	Highly polymorphic in Eurasia and N. America. Much taxonomic confusion. Diverse habitat affinities in different parts of range.	—
Leymus triticoides (Buckl.) Pilger (= *Elymus triticoides* Buckl.; *E. condensatus* J. Presl var. *triticoides* (Buckl.) Thurb.)	Beardless wildrye	Poaceae	P	WR: WA s. through CA; e. to TX, CO, WY, MT: also in HI	G	W	SI/P	.	Fryxell 1957	Barkworth & Dewey (1985) report *Leymus* species are usually outcrossing polyploids with long anthers.	—
Nassella viridula (Trin.) Barkworth (=*Stipa viridula* Trin.)	Green needlegrass	Poaceae	P	WR: AZ, CA, CO, ID, IL, IA, KS, MN, MT, NE, NM, NY, ND, SD, UT, WI, WY	G, V	W	SC/P	.	Johnson & Rogler 1943, Jones & Nielson 2004	Forms natural hybrids with *Acnatherum hymenoides*	—
Panicum virgatum L.; Two varieties: 1) *P. v.* var. *virgatum*; 2) *P. v.* var. *spissum* Linder	Switchgrass	Poaceae	P	1) G: N. America, mostly e. of Rocky Mtns. (not in CA, OR, WA, MN), s. Canada, s. to MEX, Cuba, Bermuda, and Costa Rica. 2) R: restricted to n.e. US, RI north, PE east.	G, V?	W	SI/P	Common garden-provenance tests and latitudinal adaptation, genetics of cultivars, variation in cytotypes, cytotype incompatibility, population differentiation and genetic variability	Hopkins et al. 1995; Martinez-Reyna et al. 2001; Martinez-Reyna & Vogel 2002; Vogel Casler et al. 2004; Das et al. 2004; Smart et al. 2004	Outcrossing but also facultative apomict (Frankel & Galun 1977). Studies on quantitative genetic variation for agronomic traits, e.g., forage yield, leaf elongation. Looking for heritable traits to select on (Das et al. 2004). Possible late acting "S-Z" incompatibility system (Matinez-Reyna et al. 2002. A postzygotic system also prohibits mating between octaploid and tetraploid plants.	—
Pascopyrum smithii (Rydb.) A. Löve (=*Agropyron smithii* Rydb.)	Western wheatgrass	Poaceae	P	G: Canada south to CA and TX, east to TN, MI, WI, and NY		W					—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Poa alpina L.	Alpine bluegrass	Poaceae	P	WR: AK to s. Canada; WA, OR, ID, MT, WY, CO, UT, NM, MI		W	apomixis	Seed germination and growth of clones from different provenances, alpine restoration	Hermesh & Acharya 1992	Primarily apomictic, sometimes sexual and outcrossing (Fryxell 1957)	—
Poa secunda J. Presl (Includes all former forms, varieties, subspecies, and species in *P. secunda/P. scabrella* complex; e.g., in N. Amer. = *P. ampla* Merr., *P. canbyi* (Scribner) Howell , *P. juncifolia* Scribner, *P. gracillima* Vasey, *P. nevadensis* Vasey ex Scribner, P. sanbergii Vasey, *P. scabrella* (Thurber) Ponert) *Most literature uses old names.*	Sandberg bluegrass, Canby bluegrass, and big bluegrass	Poaceae	P	G: AK to northern MEX, much of s. Canada; ME, MI, SD, WI, SD, NE, CO, OK, and NM west to Pacific Coast; disjunct in Chile	W	W	SC, and apomixis	Reproductive biology, cytology, biosystematics and morphological variation, hybridization, and common gardens, AFLP variation of cultivars and natural populations	Arnow 1981; Hiesey & Nobs 1982; Kellogg 1985, 1987, 1990; Soreng 1991; Larson et al. 2001; Ogle et al. 2003	In CA study with local plantings, *P. secunda* , showed lower competition with a rare annual plant than did exotic grasses. All grasses reduced biomass of the rare plant (Carlsen et al. 2000). Hiesey & Nobbs (1982) crossed and planted *P. scabrella* x *P. ampla*, *P. canbyi* x *P. ampla, P. gracillima* x *P. scabrella* (all now considered *P. secunda)* , and *P. scabrella* with other *Poa* species in common gardens. Inter specific crosses sometimes fertile (fertile F2s).	—
Pseudoroegneria spicata (Pursh) A. Löve *(= Agropyron spicatum* (Pursh) Scribn. & J.G. Sm.; *Elytrigia spicata* (Pursh) D.R.Dewey); Two subsp. in R2: 1) *P. s.* ssp. *spicata* ; 2) *P. s.* ssp. *inermis* (Scribnl. & J. G. Smith) A. Löve (= *A. inerme* (Scribn. & J.G. Sm.) Rydb.)	1) bluebunch wheatgrass; 2) beardless wheatgrass	Poaceae	P	1) G: AK s. to WA, OR, and CA e. to NM, CO, SD, and ND; also in MI; 2) G: s.w. Canada; WA, OR, ID, MT, WY, NV, UT, CO, NE, NM, TX		W	SI		Jensen et al. 1995, Larson et al. 2004	This species hybridizes with other related North American and Eurasion species and genera. Complex cytogenetics and hybrid sterility (e.g., Jensen et al. 1995). Subspecies hybridize (FEIS).	—

Herbs and other graminoids:

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Achillea millefolium L. Two varieties native in US: 1) *A. m.* var. *alpicola* (Rydb.) Garrett (= *A. lanulosa* Nutt. *ssp. alpicola* (Rydb.) Garrett) 2) *A. m.* var. *occidentalis* DC. (= *A. angustissima* Rydb.; *A. aspleniifolia* auct. non Vent.; *A. lanulosa* Nutt.; *A. lanulosa* var. *typica* Keck; *A. rosea* Desf.; *A. occidentalis* (DC.) Raf. ex Rydb.)	1) Common yarrow 2) western yarrow	Asteraceae	P	1) G: Western US, AK to BC, OR and CA east to MT, WY, CO, NM; 2) Canada and continental US except LA, to SC, KT and VA	W	I	SI	extensive taxonomic revisions, common gardens, cytology, crosses among taxa, within cytotypes, and among cytotypes	Clausen, Keck, & Hiesey 1940; Hiesey & Nobs 1970; Terziiski et al. 1995, Yurukova-Grancharova et al. 2002	The taxon, *A. m.* L. var. *millefolium* is native to Eurasia and introduced to many locations in the US (including KS in R2). In Bulgaria, facultative apomixis reported in studies of natural tetraploid populations and in related diploid taxa (frequency not reported). US varieties not examined.	—
Antennaria parvifolia Nutt.	Small-leaf pussytoes	Asteraceae	P	WR: mid to high elevation habitats: BC to Manitoba; WA to CA, e. to MN & MI, NE, CO, NM and OK	W	I	D	Polyploidy, differential success of apomicts and sexual plants	Bayer & Stebbins 1987, Bierzychudek 1989, FEIS	Dieocious (therefore sexual seed outcrossed) but often produce apomictic seeds.	—
Antennaria rosea Greene Four subsp: 1) *A. r.* ssp. *rosea* 2) *A. r.* ssp. *arida* (E. Nels.) Bayer 3) *A. r.* ssp. *confinis* (Greene) Bayer 4) *A. r.* ssp. *pulvinata* (Greene) Bayer	Rosy pussytoes	Asteraceae	P	WR: mid to high elevation habitats: 1) AK, WA, CA, MT, ID,WY, CO, ND, SD, MN, MI 2) AK, WA, ID, WY, CO, NM, AZ 3) AK; WA to CA, e. to MT, WY, CO, AZ 4) AK, WA to CA, ID, NV, AZ, MT, WY, CO; MN	W	I	D	Geographic pattern in allozyme and morphological variation, hybrid origin, clonal diversity, population genetics	Bayer 1990, Bayer & Stebbins 1987	Most *A. rosea* populations are clones of female plants. Highly apomictic. Note: apomixis, polyploidy, and dioecy are prevalent in this genus. Apomictic plants are always polyploid, but not vise versa (Bayer & Stebbins 1987).	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Aquilegia caerluea James (=*A. coerulea* James) Of five subtaxa , 1, 2, 3, and 4 in R2. 1) *A. c.* var. *alpina* A. Nels 2) *A. c.* var. *caerulea* James 3) *A. c.* var. *daileyae* Eastw. 4) *A. c.* var. *ochroleuca* Hook. 5) *A. c. v* ar. *pinetorum* (Tidestrom) Payson ex Kearney & Peebles	Colorado blue columbine	Ranuncula-ceae	P	1) R: WY, UT 2) WR: ID, MT, UT, NV, CO, NM, WY 3) R: CO 4) R: CO, ID, MT, WY, UT, NV; 5) R: AZ, NV, UT	G	I, some A(HB)	SC/P, DC	Quantitative genetics, inbreeding depression, pollination biology, morphological variation and geographic patterns, mating system variation	Miller 1978, 1981; Montalvo 1992, 1994; Hodges & Arnold 1994; Brunet & Eckert 1998; Brunet & Sweet 2004	Mixed mating and variable outcrossing rates (Brunet & Eckert 1998, Brunet & Sweet 2004). Self pollen tubes are about 90% as successful as outcross tubes in reaching ovules (Montalvo 1992). Plants hybridize with other species of *Aquilegia* where populations contact (e.g., *A. chrysantha* A. Gray and *A. elegantula* Greene, Miller 1978, Weber 1987, Hodges & Arnold 1994).	—
Astragalus linifolius Oster.	Grand Junction milkvetch	Fabaceae	P	S: CO	G	I	SC/P 10% autog.	Inbreeding depression	Karron 1989		—
Arabis fecunda Rollins	Mt. Sapphire rockcress	Brassicaceae	P	S: MT	G	I	SC/P	Inbreeding depression	Hamilton & Mitchell-Olds 1994	There is evidence for mixed mating system in this rare species.	—
Artemisia ludoviciana Nuttall Of eight subspecies, five occur in R2: 1) *A. l.* ssp. *ludowiciana* 2) *A. l.* ssp. *albula* 3) *A. l.* ssp. *candicans* 4) *A. l.* ssp. *icompta* 5) *A. l.* ssp. *mexicana*	White sagebrush, Louisiana sagewort	Asteraceae	P	1) G: All continental states excpt AK, FL, AL, WV; Canada from BC to Ontario 2) CA e. to CO, s. to TX; MS, OH, NY 3) WA to CA, e. to MT, WY, UT 4) WA to CA, e. to MT, WY, CO 5) CA e. to MS, AK TX	W	W, G	SC/heads P	Cytological	in Taylor & McArthur 2004	Both female and perfect flowers in same head (inflorescence). Highly polymorphic species with subshrub and herbaceous forms (Taylor & McArthur 2004). Different varieties and synonyms reported by Taylor & McArthur, shows difficult taxonomy.	—
Balsamorhiza sagittata Pursh (Nutt.)	Arrowleaf balsamroot	Asteraceae	P	WR: s. Canada, ND, SD, CO, and AZ west to Pacific states	G, V	I	—/heads perfect, DC	Possible ecotypic variation but also has broad ecological tolerance	Monsen et al. 2004	Hybridizes with other species in genus (FEIS). Seeding outside native range has not been successful, and seeding with unadapted ecotypes has been problematic (Monsen et al. 2004, Vol. 2). Seed dormancy.	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Campanula americana L. (= *Campanulastrum americanum* (L.) Small)	American bellflower	Campanula-ceae	A, B	SD south to OK, e to NY and FL, north to Ont. Canada. (throughout eastern US)	G	I, S	SC/P, DC	Life history variation, quantitative genetics, genetic basis of crossing success, pollinators and floral trait preferences	Kalisz & Wardle, Galloway 2001a,b, Galloway & Etterson 2004, Lau & Galloway 2004	Complex seed germination: season of germination determines if annual or biennial. Large maternal effects on germination, but also effects of father. Some flowers readily self in greenhouse, but flowers protandrous.	—
Campanula rotundifolia L.	Harebell, bluebell bellflower	Campanula-ceae	P	G: Circumpolar AK, Canada, most of US except NV, KS, OK, s.e. and KY	W?	I (bees)	SC/P	Genetic diversity, pollination, soil seed bank size	Bingham & Ranker 2000, Alsos et al. 2003	No population structure between a high and low elevation population in CO (Bingham & Ranker 2000). Seedbanking is variable.	—
Carex scopulorum Holm. Of three varieties, first two in R2: 1) *C. s.* var. *scopulorum* 2) *C. s.* var. *bracteosa* (Bailey) F.J Herm. 3) C. s. var. *pruinophylla* (Holm.) L.A. Standley	Rocky Mountain sedge	Cyperaceae	P	1) WR: WA to CA east to Rocky Mtns., CO; 2) WR: BC and Ykon T., Canada, CA, CO, ID, MT, OR, WA, WY; 3) BC, ID, MT, WA	G	I,W?	SC/M	Population differentiation, clonal diversity	Linhart & Gehring 2003	Flowers unisexual, mostly in separate spikes; plants monoecious.	—
Chamaecrista fasciculata (Michx.) Greene (= *Cassia fasciculata* Michx.); Of two varieties, only #1 in R2: 1) *C. f.* var *fasciculata* 2) *C. f.* var. *macrosperma* (Fern.) C.F. Reed	Partridge pea, sleeping plant	Fabaceae	A	G: s. Ontario, MN, MA, south to CO and KS 1) G: east of Rocky Mtns.: from Ontario, SD s. to TX and NM, e. to Atlantic and Gulf coasts, except MN, NH, VT; 2) R: VI, DE	E, G	I (large bees)	SC/P	Inbreeding and outbreeding, population structure, pollination, outcrossing rate	Fenster & Sork 1988, Fenster 1991a,b,c; Fenster & Galloway 2000, Etterson & Shaw 2001, Etterson 2004a,b	After fire, this annual plant reproduces from seeds scarified by fire. It tends to increase after fire (FEIS).	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Chamerion angustifolium (L.) Holub (=*Epilobium angustifolium* L., *Chamaenerion angustifolium* (L.) Scop.) Two subspecies: 1) *C. a.* ssp *angustifolium* 2) *C. a.* ssp *circumvagum* (Mosquin) Kartesz, comb. nov. ined.	Fireweed	Onagraceae	P	Species circumpolar 1) G: Canadian: all provinces; in US: AK, WA, MT, WY; 2) G: in US: AK; WA to CA, e. to NM, CO, and NE, and from NE e. to Atlantic coast, s to KY and TN	W	I	SC/P,DC	Common garden, variation in ploidy, geographic variation, adaptation, inbreeding depression	Clausen, Keck & Heisey 1940, Myerscough 1980, Husband & Schemske 1995, 1998, Parker et al. 1995, Burton & Husband 2000, Husband et al. 2002	Gene flow potential high. Flowers require pollinators (primarily bumblebees in day, hawkmoths at night) for seed set (Meyerscough 1980). Seeds capable of long distance wind dispersal as evidenced by colonization of volcanic areas on islands and in seed traps on Mt. St. Helens (Parker et al. 1995). Ranges of morphological variation of the two subspecies overlap--the distinguishing feature is chromosome number (*C. a.* ssp. *angustifolium* is diploid).	—
Collomia linearis Nutt.	Collomia	Polemoni-aceae	A	G: AK to QU, s to MN, CO, AZ and CA	G	I (S)	SC/P	Seed and pollen dispersal	Wilken 1977	Greenhouse test for phenotypic plasticity and local trait differentiation of populations from two environments.	—
Dalea candida Michx. Ex Willd. 1) *D. c.* var. *candida* 2) *D. c.* var. *oligophylla* (Torr.) Shinners (= *D. oligophylla* (Torr.) Shinners)	White prairieclover	Fabaceae	P	1) G: ND e. to WI, s. to TX, LA, MS, AL, GA, SC through SD, KS, IL, IN; southern Alberta and Ontario, Canada, and n. MEX 2) G: MT e. to MN, s. through Great Plains to AZ, NM, TX	G	I	—/P			Important prairie plant. Also used in ornamental horticulture.	—
Dalea purpurea Vent. two varieties: 1) *D. p.* var. *purpurea* 2) *D. p.* var. *arenicola* (Wemple) Barneb	P	Fabaceae	P	1) G: MT, e to NY, s to AZ, NM, TX, LA, MO, AL 2) WR: CO, NM, TX, NE, KS, OK	G	I	—/P	Genetic diversity, differential competitive ability	Gustafson et al. 2002	Fire increases seed germination (FEIS). Low levels of inbreeding indicated from genetic marker analysis ($F_{IS} = 0.120$) suggest the species is highly outcrossing. Remnant prairie populations were found to harbor more RAPID variation than restored populations	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Delphinium nuttallianum Pritzel ex Walpers (=*D. nelsonii* Greene)	Nelson's larkspur, two lobed larkspur	Ranuncula-ceae	P	WR: WA to CA, e. to MT, SD, NE, CO, NM	I	G	SC/P/DC	Outbreeding and inbreeding depression, flower color adaptation, population structure, pollination biology	Price & Waser 1979, Waser 1982, Waser & Price 1994, Williams & Waser 1999, Schulke & Waser 2001, Bosh & Waser 2001	Pollen dispersal studies. Pollinators tend to fly short distance between flowers, but longer distance flights occur between patches of plants. Self pollination did not vary between sparse and dense arrays of plants.	—
Erythronium grandiflorum Pursh Of four subspecies, two in R2: 1) *E. g.* ssp. *grandiflorum* 2) *E. g.* ssp. *chrysandrum* *A*pplegate	Glacier lily, yellow avalanche-lily	Liliaceae	P	1) WR: BC and Alberta, Canada; WA, OR, CA, ID, MT, WU, UT 2) WA, ID, UT, WY, CO, NM	G	I	SC/P	Crosses between subspecies, pollen flow, pollen competition, pollination, inbreeding effects	Fritz-Sheridan 1988, Cruzan 1990, Rigney et al. 1993, Rigney 1995	Inbreeding depression observed very early in life cycle. Inbred ovules tend to abort. This may be confused with self-incompatibility. Variation in pollen color (red vs. yellow). Corms eaten by mammals.	—
Gaillardia pulchella Foug. Of three varities, one in R2: 1) *G. p.* var. *pulchella*	Blanket flower, fire-wheel	Asteraceae	A, P	1) G: All continental states except WA, OR, ID, UT, MT, WY, ND and several small eastern states	W	I	SI/P	Chromosome differentiation, biparental inbreeding depression, edaphic races, allozyme variation, genetic diversity	Stoutamire 1955, 1977, Heywood & Levin 1984, 1985, Heywood 1993	Chromosomal races. Highway plantings in TX for many years (at least 1950s) have increased dispersal.	—
Geranium caespitosum James Of four varieties, three in R2: 1) *G. c.* var. *caespitosum* 2) *G. c.* var. *fremontii* (Torr. ex Gray) Dorn 3) *G. c.* var. *parryi* (Engelm.) W.A. Weber	James geranium	Geraniaceae	P	1) G: NV, UT, WY, CO, NM, TX 2) NV, WY, UT, CO, AZ, NM 3) WY, UT, CO, AZ, NM	G, V	I (bees)	SC/P, DC	Common garden (plasticity), pollination, inbreeding depression, population differentiation	Clausen, Keck & Heisey 1940; Hessing 1988, 1989 a, b		—
Impatiens capensis Meerb.	Jewelweed	Balsamin-aceae	A	WR: WA, OR, ID; CO; ND south to TX and e. in all midwest, eastern and southern states	E, G	I	SC/P,CL	Inbreeding depression, quantitative genetics, outcrossing rates, inbreeding levels, population structure	Mitchell-Olds & Waller 1985, Mitchell-Olds 1986, Knight & Waller 1987, Schmitt & Gamble 1990	Plants have mixture of cleistogamous and chasmogamous flowers. Strong maternal effects found in first month of growth (McCall et al. 1991).	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Ipomopsis aggregata (Pursh) V. Grant 1) *I. a.* ssp. *aggregata* 2) *I. a.* ssp. *attenuata* (Gray) V.& A. Grant 3) *I. a.* ssp. *bridgesii* (Gray) V.& A. Grant 4) *I. a.* ssp. *candida* (Rydb.) V.& A. Grant 5) *I. a.* ssp. *collina* (Greene) Wilken & Allred 6) *I. a.* ssp. *formosissima* (Greene) Wherry 7) *I. a.* ssp. *weberi* V. Grant & Wilken	Scarlet gilia	Polemon-iaceae	S, P	1) P: WY, CO 2) WR: WA, ID, MT, CO, NV, UT 3) P: CA 4) P: CO, NM 5) P: CO, NM 6) WR: WA, OR, CA, NV, UT, CO, AZ, NM, TX, OK 7) P: ID, WY, CO	G	A (HB), I	SI/ P	Pollination biology, outbreeding and inbreeding depression, floral trait selection, gene flow, hybridization, geographic differentiation	Waser 1982, Waser & Price 1989, Wolf & Soltis 1992; Campbell et al. 1997, Heschel & Paige 1995, Grant 1992, Caruso 2001	Pollen dispersal studies. Pollinators tend to fly short distance between flowers (< 1 m). Hybridization and hybrid zones and hybrid swarms with related species-- *I. tenuituba* . Cambell et al. 1997 found evidence for directional selection. Hummingbirds over visi+K55ted the red *I. aggregatta* and flowers with wide corolla tubes while hawkmoths overvisited the light and narrow tubed *tenuituba*. Hybrids suffered disadvantage.	—
Liatris punctata Hook. Of three varieties, two are in R2: 1) *L. p.* var. *punctata* 2) *L. p.* var. *nebraskana* Gaiser	1) Dotted blazing star 2) Nebraska blazing star	Asteraceae	P	1) MT e. to MN; s. to NM, TX, OK; IL 2)MN, IL, MI, SD, NE, KS, OK, CO, NM, TX, LA, MO, TN	W	I	—/heads P			Most common nectaring foodplant of federally threatened Pawnee Mountain Skipper in Colorado study (Wooley et al. 1992).	—
Linum lewisii Pursh Only the first (#1) variety in R2: 1) *L. l.* var. *lewisii* 2) *L. l.* var. *alpicola* Jepson (not in R2)	Lewis blue flax (Lewis flax, blue flax)	Linaceae	P	1) WR: AK to MEX and e. to WI, MI, NE, KS, AR, LA. In US, mostly west of Mississippi R. 2) P: ID, CA, NV, UT	G, A	I	SC/P	Common garden, variation in morphology, and seed germination (see Table 10.7)	Meyer & Kitchen 1994, 1995, Kichen 1994, Okendon 1968, Munz & Keck 1968	Also considered a subshrub.	—
Lobelia cardinalis L.	Scarlet lobelia, cardinal flower	Campanula-ceae	P	WR: moist places continental North America, MEX, Central America (except AK, OR, WA, ID, MT, WY, ND, SD)	G, W	A (HB)	SC/ P	Inbreeding and outbreeding depression, trait plasticity, hybridization, selection on floral traits	Witherspoon 1974, Devlin 1988, 1989, Johnston 1991, 1992, 1993 , Schlichting & Devlin 1992, Johnson 2003	Natural hybridization with *L. siphilitica* (Witherspoon 1974). Experimental evidence for local adaptation, gene flow from cultivated to wild populations, and establishment of heterotic F1 hybrids (Johnson 2003). Evidence for pollinator selection on floral traits.	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Lobelia siphilitica L. 1) *L. s.* var. *ludoviciana* A. DC. 2) *L. s.* var. *siphilitica*	Great blue lobelia	Campanulaceae	P	1) WR: moist places in central US: WY, ND, MN, WI s. to TX, LA, MS 2) WR: moist places in e. US states except FL, w. to MO, AR, MN, SD	G, W	I (bees)	SC/ P or G	Inbreeding and outbreeding depression, selection on floral traits, breeding system, trait plasticity, genetic variation in floral traits, hybridization, genetics of cytoplasmic male sterility	Witherspoon 1974, Johnston 1991, 1992, Pigliucci & Schlichting 1995, 1997, Mutikainen & Delph 1998, Dudle et al. 2001, Caruso 2004	Plant of wet sites. Natural hybridization with *L. cardinalis* (Witherspoon 1974). Occurrence of gynodioecy and protandry, encourages outcrossing. Experimental evidence for genetic variation in plasticity of traits in response to light and nutrients.	—
Mertensia ciliata (James ex Torr.) G. Don 1) *M. c.* var. *ciliata* 2) *M. c.* var. *stomatechoides* (Kellogg) Jepson	Tall mertensia, tall fringed bluebells	Boraginaceae	P	1) P: NV, ID, MT, WY, SD, UT, CO, NM, AZ 2) P: OR, CA, NV	G	I	—/P				—
Mimulus guttatus de Candolle (inlcudes *M. nasutus* Greene and *M. micranthus* which are treated as separate species in most experimental studies)	Common yellow monkeyflower, seep monkeyflower	Scrophulariaceae	P, A	G: In damp areas and seeps: AK to CA and MEX, e. to ND, SD, NE, CO, NM; MI, NY, PA	water (W)	I	SC/P	Population genetics, heavy metal adaptation, plasticity, inbreeding depression, mating system, quantitative genetics, selection by herbivores	Vickery 1958, Waser et al. 1982, Ritland & Ganders 1987a,b, Dole & Ritland 1989a,b, 1993, Searcy & McNair 1990, Galloway 1995, Macnair & Cumbs 1989, Dudash & Carr 1998, Fishman et al. 2002, Swiegart & Willis 2003, Ivey et al. 2004	The many synonyms in PLANTS database show there is great variation in this species. Many ecological genetics studies exist that justify separation into more than one species. Mixed mating species with much variation in outcrossing rate exist. The closely related *M. nasutus* and *M. micranthus* have smaller flowers and are primarily selfing. Plants hybridize with *M. nasutus* where ranges overlaps and there is evidence for asymmetrical introgression (Fishman et all. 2002). The PLANTS database lumps these species into one species. Naturalized in Europe.	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guidelines
Mimulus lewisii Pursh.	Purple monkeyflower	Scrophulariaceae	P	P: AK to WA; OR, CA, ID, NV, MT, WY, CO	W	I	SC/P	Hybridization, introgression, cytology, adaptation to pollinators and habitat, reproductive isolation, seed germination patterns	Vickery 1958, Vickery & Anderson 1967, Pollock et al. 1967, Hiesey & Nobs 1971, Meyer & Kitchen 1994, 1995, Kichen 1994, Bradshaw et al. 1995, Ramsey et al. 2003	Many experimental studies exist involving this bee-pollinated species of high elevations and latitudes and the closely related hummingbird-pollinated *M. cardinalis* of generally lower elevations and latitudes. The studies provide a classic example of pollinator influenced selection on floral traits and reproductive isolation in zones of overlap. These results are coupled with adaptation to different physical environments.	—
Penstemon strictus Benth.	Rocky Mountain penstemon	Scrophulariaceae	P	WR: southern WY, CO, UT, NM, northeastern AZ	G	I	—/P	Seed germination	Hooks & Oaks 1982, Meyer & Kitchen 1994	Seed dormancy of 'Bandera' differs from that of native seed accession from different origin (Meyer & Kitchen 1994).	—
Polemonium viscosum Nutt.	Sky pilot, sticky polemonium	Polemoniaceae	P	P: high elevation in Canada (Alberta to BC), s. to NM, AZ, OR	G	I (bee)	SI/ P	Pollination, seed predation, common garden, population structure	Galen & Kevan 1980, Galen 1989, 1999, 2000, Galen et al. 1999	Examined clinal variation and population differentiation in floral and other traits over elevation gradient. Pollinator and ant mediated selection on flower traits.	—
Polygonum viviparum L.	Alpine bistort	Polygonaceae	P	WR at high latitudes or high elevation: AK to WA, OR, MT, ID, NV, UT, CO, NM, SD, MN, MI, M; northern Europe	G	I	—/P, bubils	Sexual versus clonal reproduction, clonal diversity, adaptation to high altitude	Diggle et al. 1998, Bauert 1996, Bauert 1993	Tiny, asexual bulbils replace few to many flowers. Clonal and polyploid (2n= 96). Seeds have not been observed in North America and only rarely in Europe.	—

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Potentilla glandulosa Lindl. Of eleven subsp., three in R2: 1) *P. g.* ssp. *glabrata* (Rydb.) Keck 2) *P. g.* ssp. *micropetala* (Rydb.) Keck 3) *P. g.* ssp. *pseudorupestris* (Rydb.) Keck	Sticky cinquefoil	Rosaceae	P	1) WR: WA, OR, NV, ID, UT, AZ, MT, WY, CO, SD, 2) WR: ID, NV, UT, WY 3) WR: WA, ID, WA, OR, CA, NV, UT, CO	GR	I	—/P	Common garden	Clausen, Keck & Heisey 1940		—
Potentilla gracilis Dougl. ex Hook. ssp. *fastigiata* (Nutt.) S. Wats. (=*Potentilla gracilis* Dougl. ex Hook. ssp. *nuttallii* (Lehm.) Keck)	Slender cinquefoil	Rosaceae	P	G: AK south to Baja CA, east to MN and MI, WY, CO, NM	G	I	—/P		Clausen, Keck & Heisey 1940		FSH
Scutellaria brittonii Porter	Britton's skullcap	Lamiaceae	P	P: WY, CO, NM, NE, KS	G	I	SC/P	population structure	Olmstead 1990	Mixed mating.	FSH
Solidago gigantea Ait.	Late goldenrod	Asteraceae	P	G: Newfoundland to BC, south to all US states except AZ	W	I	—/heads P				FSH
Trillium grandiflorum (Michaux) Salisbury and *T. erectum*	White trillium and red trillium	Liliaceae	P	P: eastern North America	I (ants)	I	SC/P	Effects of crossing distance, mating system	Irwin 2001, (Lubbers & Lechowicz 1989 for natural history of *T. g*.)	Found inbreeding depression (selfing produces few seeds), but no outbreeding depression in seed production within 1500 m crossing distance (limit of distance test). Not in R2.	FSH
Subshrubs:											FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Artemisia frigida Willd.	Fringed sage	Asteraceae	P	G: AK s. through Canada and south primarily in states w. of Mississippi R. except OR, CA, and OK; occurrences in MI, NY, VT, PA, CT, MA, NJ; Siberia, Europe, Asia	G (W)	W	—/P	—	—	Perhaps the most widely distributed and abundant species of *Artemisia*. Plants establish substantial seedbank (FEIS). FEIS refers to possible ecotypes. McArthur and Taylor (2004a) note much variation and three varieties, but a constant number of chromosomes. No studies on genetic variation.	FSH
Sphaeralcea coccinea (Nutt.) Rydb. 1) *S. c.* ssp. *coccinea* 2) *S. c.* ssp. *elata* (E.G. Baker) Kearney	Scarlet globemallow	Malvaceae	B, P	1) WR: BC Cananda to Manitoba, south and eastward to NM, TX, and MEX 2) WR: WY, south to NM, TX and west to NV and AZ.	G (V)	I	—/P	common garden	Pendery & Rumbaugh 1990	Self-sterility is common in *Sphaeralcea* (Pendery & Rumbaugh 1990).	FSH
Stanleya pinnata (Pursh) Britton; two varieties in CO: 1) *S. p.* var. *bipinnata* (Greene) Rollins 2) *S. p.* var. *integrifolia* (James) Rollins	Prince's plume, desert plume	Brassica-ceae	P	WR: CA east to WY, KS, TX	G	I	P	Common environment	Feist & Parker 2001	Selenium accumulator for bioremediation.	—
Shrubs:											
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roemer Two of four varieties in R2: 1) *A. a.* var. *alnifolia* 2) *A. a.* var. *cusickii* (Fern.) C.L. Hitchc	1) Saskatoon serviceberry 2) Cusick's serviceberry	Rosaceae	P	1) WR: AK s. through Canada to nw US: WA, OR, ID, NV, MT, WY, CO, ND, SD, NE, MN, IA 2) WR: WA, OR, NV, ID, MT, WY	A, V	I	/P		FEIS	Much variation and intergradation of forms.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Arctostaphylos uva-ursi (L.) Spreng.	Bearberry, kinnikinnick	Ericaceae	P	WR: AK s. through Canada, all US states west of MT, WY, CO, NM; all Great Lakes states, and n.e. states from ME to NJ; VA	V, A	I	/P				FSH
Artemisia tridentata Nutt. Four of six subspecies are native to R2: 1) *A. t.* ssp. *tridentata* 2) *A. t.* ssp. vaseyana (Rydb.) Beetle 3) *A. t.* ssp. wyomingensis Beetle & Young 4) *A. t.* ssp. *spiciformis* (Osterhout) Kartesz & Gandhi	1) Basin big sagebrush 2) mountain big sagebrush 3) Wyoming big sagebrush 4) big sagebrush	Asteraceae	P	1) G: MT s to NM and w. to Pacific states 2) WR: WA e. to ND, SD, NE; s. to CA, NV, UT, CO 3) WR: MT, ND, SD, NE, WY, CO, UT, NV, AZ, OR, CA 4) P: WA, ID, MT, WY, CO, UT, NV, CA	W	W	SI/P	Provenance trials, hybrid zones and fitness, variation in seed germination and seedling survival, ploidy	Meyer & Monsen 1990, 1991, 1992, Graham et al. 1995, Wang et al. 1997, 1999	Draft seed transfer guidelines (Mahalovich 2003, Mahalovich & McArthur 2004)	FSH
Atriplex canescens (Pursh) Nutt. one of six varieties native to R2: 1) *A. c.* var canescens	Fourwing saltbush	Chenopod-iaceae	P	G: southern Alberta and Sask. Canada; western US from OR e. to ND, south to Baja California, TX, MEX	W	W	na/D (M)	Provenance tests, geographic distribution of ploidy levels, breeding system, phytochemistry, hybridization among cytotypes and species, cultivar releases	Sanderson & McArthur 2004, Stutz et al. 1979, Pendleton et al. 1992	Seed transfer zones available (Sanderson & McArthur 2004). Four races recognized. Recommend using wildland collected materials within zones of adaptation (included chromosomal race). Cultivars can be considered in areas to which they are adapted.	FSH, YES
Cercocarpus montanus Raf. Two of seven varieties in R2: 1) *C. m.* var. *montanus* 2) *C. m.* var. *argenteus* (Rydb.) F.L. Martin	1) Mountain mahogany 2) Silver mountain mahogany	Rosaceae	P	1) WR: OR, ID, MT, NV, UT, WY, SD, CO, NE, KS, OK, AZ, NM 2) P: CO, NM, TX	W (V)	W	/P	Hybridization among species	FEIS, Kitchen 2004	In a review, Kitchen (2004) reports F1 hybrids with *C. ledifolius* Nutt. var. *ledifolius* are fertile and backcross with parents while hybrids with *C. ledifolius* var. *intermontanus* N. Holmgren are sterile. There may also be ecotypic variation for resprouting ability.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Chrysothamnus viscidiflorus (Hook.) Nutt. Four of five varieties in R2: 1) *C. v.* ssp. *viscidiflorus* 2) *C. v.* ssp. *axillaris* (Keck) L.C. Anders. 3) *C. v.* ssp. *lanceolatus* (Nutt.) Hall & Clements 4) *C. v.* ssp. *puberulus* (D.C. Eat.) Hall & Clements	Low rabbitbrush, yellow rabbitbrush	Asteraceae	P	1) G: WA s. to CA; e. to MT, and s. to NM; NE 2) WR: CA, NV, UT, CO, AZ 3) G: WA s. to CA; e. to MT, and s. to NM 4) WR: WA, OR, CA, ID, NV, UT, CO, NM, AZ	W	I	/P	Polyploidy and adaptation	Anderson 1986	Highly polymorphic species with great ecological amplitude and subspecific variation (McArthur & Taylor 2004b).	FSH
Cowania stansburiana Torr. (in PLANTS=*Purshia stansburiana (Torr.) Henrickson*)	Stansbury cliffrose	Rosaceae	P	AZ, CA, CO, ID, NM, NV, to MEX	W	I	/P			*Cowania* has undergone a revision and has been combined into *Purshia* . Occasional plants with male flowers and perfect flowers.	YES
Ericameria nauseosa (Pallas ex Pursh) Nesom & Baird (=*Chrysothamnus nauseosus* (Pallas ex Pursh) Britt.) 1) *E. n.* ssp. *nauseosa* 2) *E. n.* ssp. *consimilis* (Greene) Nesom & Baird	Rabbit brush, rubber rabbitbrush	Asteraceae	P	1) G: Entire western half of the US and Canada: WA s. to CA; e. to ND and s. to TX 2) G: OR, CA, ID, NV, UT, WY, CO, AZ, NM	W	I	/P	Provenance tests, seed germination variation	Meyer et al. 1989, Mayer & Monsen 1990, McArthur and Taylor 2004c	An extremely variable species with many subspecific taxa. Four of eight varieties of *E. n.* ssp. *consimilis,* and five of 14 varieties of *E. n.* ssp. *nauseosa* are listed in PLANTS as in R2. Some subspecies separated by elevation. Seed germination varies depending on source.	YES
Purshia tridentata (Pursh) DC.	Antelope bitterbrush	Rosaceae	P	G: BC, Canada to WA, OR, ID, MT, south to eastern CA, AZ, and NM, including western CO; n. Baja CA	W (V)	I	SI/P	Hybridization, adaptability of 'Lasen' tested in many western states, genetics of seed dormancy	Shaw & Monsen 1986, Meyer & Pendleton 2000	Hybridizes and introgresses, with cliffrose (*Cowania stansburiana*) where the species overlap (McArthur et al. 1983). Transfer guidelines (Mahalovich 2003).	YES
Rhus glabra L.	Smooth sumac	Anacard-iaceae	P	In all 48 contiguous US states, Canada, n. Mexico, (rare in CA)	A	I	/	Allozyme study, seed predation	Chung & Waller 1986, Sherman-Broyles et al. 1992	Widespread. Considered aggressive-invasive in some locations.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Rhus trilobata Nutt. Three of six varieties occur in R2: 1) *R. t.* var. *trilobata* 2) *R. t.* var. *pilosissima* Engelm. 3) *R. t.* var. *simplicifolia* (Greene) Barkl.	1) Skunkbush sumac 2) Pubescent skunkbush sumac 3) Skunkbush sumac	Anacard-iaceae	P	1) G: Western US except WA; OR e. to MT, south to TX and CA; also AR 2) G: CA, AZ, NM, TX, CO, KS, OK 3) G: OR, CA, NV, UT, CO, OK, NM,	G, V	I	/ P, M			Flowers can be perfect or unisexual.	FSH
Rosa woodsii Lindl. Two of four varieties in R2: 1) *R. w.* var. *woodsii* 2) *R. w.* var. *ultramontana* (S. Wats.) Jepson	Woods rose	Rosaceae	P	1) WR: AK s through BC and Alberta Canada, MT and WY e. to WI; NE, KS, OK, TX, NM, AZ 2) WA, OR, ID, MT, CA, NV, UT, CO, NM	A, V	I	/P				FSH
Quercus gambelii Nutt. Two varieties, one in R2: 1) *Q. g.* var. *gambelii*	Gambel oak	Fagaceae	P	WR: NM west to AZ and s.w. NV, north to UT, CO and southeastern WY, SD; isolated patches occur in TX, OK, and MEX	A (V)	W	SI(maybe)/ M	Hybridization, hybrid zones and herbivores, clonal structure, genetic diversity, population structure (allozymes or VNTR DNA)	FEIS; Campbell & Boecklen 2002; Schnabel & Hamrick 1990 a, b; Kumar & Rogstad 1998	Oaks do not produce seeds from self-pollination. They are highly outcrossing. Extensive review of hybrid zones and zones of contact found that vertebrate diversity was higher in areas of contact than in hybrid zones (Campbell and Boecklen 2002). Hybridizes with *Q. arizonica*, *Q. macrocarpa*, *Q. muehlenbergii*, *Q. grisea*, *Q. mohriana*, and *Q. turbinella* (FEIS).	FSH
Salix brachycarpa Nutt.	Gray-leaf willow	Salicaceae	P	WR: mesic areas AK, w. Canada, CA, CO, ID, MT, NM, OR, UT, WA, WY	W	I	D			Insect pollinated. Dioecy enforces outcrossing.	FSH
Salix exigua Nutt.	Sandbar willow, coyote willow	Salicaceae	P	WR: mesic, riparian areas in western US: NE, TX; MT s to NM, and w to ocean.	W	I	D		FEIS, Nellessen 2004	Dioecy enforces outcrossing. Spreads and stabilizes stream banks. Variable species complex; three subp And twice as many varieties have been named.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Salix scouleriana Barratt ex Hook.	Scouler willow	Salicaceae	P	WR: mesic upland and riparian; AK and western N Amer. SD; MT s. to NM and west to coast.	W	I	D		Francis 2004	Most common upland willow in much of its range. Large range of elevations.	FSH
Sorbus scopulina Greene	Greene's mountain ash	Rosaceae	P	WR: AK, Yukon, Northwest Terr., BC, Alberta, Sask, MT, ID, WA; less in OR, CA, WY, ND, SD, UT, CO, NV, NM	V, A	I	P/				FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Trees, cone bearing:											FSH
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr. var. *concolor*	White fir, Rocky Mountain white fir	Pinaceae	P	WR in mountains: WY, ID, OR, NE, UT, CO, AZ, NM, and n MEX	W	W	SC/M		FIES, Fowells 1965, Sturgeon et al. 1980, Farris & Mitton 1985	Occurs above 1500 m in mesic forests of all major mountain ranges of sw. *A. c.* var. *lowiana* (Gord. & Glend.) Lemmon occurs in CA, w UT, s OR, and n Baja CA. Highly flammable and intolerant of fire, especially when young; seeds establish in understory (FEIS).	FSH
Juniperus communis L. var. *depressa* Pursh (= *J. canadensis* Lodd. ex Burgsd., *J. c.* L. ssp. *depressa* (Pursh) Franco, J. *depressa* (Pursh) Raf.)	Common juniper	Cupress-aceae	P	WR: All mainland states except NE, OK, MO s to LA, and TX e to TN, AL, and FL; Canada	A, V	W	D		.	Sex ratio can be variable. Weber (1987) recognizes *J. c.* ssp. *alpina* for CO. FT in IL and KY; FE in OH and MD.	FSH
Picea engelmannii Parry ex Engelm.	Engelmann spruce	Pinaceae	P	WR: BC and Alberta Canada, MT, WY, CO and NM, west to Pacific states	W	W		Hybridization, common garden test	Fowells 1965, FEIS, Rehfeldt 1994	Occurs in at high and cold elevations. Contradictory reports that hybridizes with Colorado blue spruce and Sitka spruce. No races or geographic varieties recognized (FEIS), but horticultural selections exist. Fire intolerant. Colonize by seed dispersal after fire.	FSH
Picea pungens Engelm.	Blue spruce, Colorado blue spruce	Pinaceae	P	P: AZ, CO, ID, NM, UT, WY	W	W		Common garden test	FEIS, Rehfeldt 1994	Putative hybrids with Engelmann spruce in MT (FEIS). PLANTS says also occurs in ME, MA, MD, NY, PN, but this appears to be an error. Typically occurs at mid elevations and is fire intolerant. Colonize by seed dispersal.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Pinus albicaulis Engelm.	Whitebark pine	Pinaceae	P	P: CA, OR, WA, NV, MT, WY; BC and Alberta, Canada	A	W	SC/M	Allozyme population differentiation, seed dispersal by Clark's nutcracker, hybridization	Jorgensen and Hamrick 1997, Bruederle 1998, Rogers et al. 1999	Subalpine distribution. Rare hybrids with limber pine infertile. Birds cache seeds from same trees in close proximity. Clusters of related trees (full and half siblings) may result in inbreeding (see FEIS).	FSH
1) *Pinus contorta* var. *latifolia* Engelm. ex S. Wats 2) *P. c.* var. *murrayana* (Grev. & Balf.) Engelm.	Lodgepole pine	Pinaceae	P	WR: Saskatchewan Canada to AK, s to CA and CO	A, V	W	SC/M	Fst vs Qst in var. *latifolia* , provenance test in var. *contorta* , hybridization with jack pine, geographic variation in closed vs. open cones, ecological genetics of Rocky Mountain populations	Wheeler & Guries 1987, Rehfeldt 1988, Yang et al. 1996, Sorenson 2001	*P. c.* var. *murrayana* (in CO)	YES
Pinus edulis Engelm.	Pinyon pine, twoneedle pinyon	Pinaceae	P	WR: Primarily in UT, CO, AZ and NM extending into CA, TX, WY, OK, and Baja CA	A, V	W	SC/M (funtional sex change from herbivory)	Allozyme variation, local and broad scale, genetic differentiation and edaphic patterns, seed dispersal	Ligon 1978, Mopper et al. 1991, Mitton et al. 1998, Mitton & Duran 2004	Highly outcrossing. In AZ study, trees susceptible to insect attack were significantly less heterozygous at allozyme loci than resistant trees. Seeds distributed and cached by Pinon jays (*Gymnorhinus cyanoephalus*) in locations conducive to germination and growth (Ligon 1978). The breeding cycle of the pinon jays in the sw U.S. is dependent on conifer seeds. The birds can carry over 50 seeds of pinon pine in their throats in one trip and can disperse seeds long distances.	YES

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Pinus flexilis James	Limber pine	Pinaceae	P	P: mostly high elevation, Alberta to CA, s. to TX and AZ	A	W	SC/M	Allozyme, mtDNA, cpDNA, RAPD, population structure, gene flow, phylogeography, geographic variation in cones and seed predators	Schuster et al. 1989; Latta & Mitton 1997, 2000; Schuster & Mitton 2000; Jorgensen et al. 2002, Mitton et al. 2000, Marshall et al. 2002.	Phylogeographic studies using mtDNA, cpDNA and allozymes (Latta and Mitton 1997, Mitton et al. 2000) showed gene flow of nuclear and chloroplast genes substantial via pollen dispersal. Gene flow from dispersal of seeds was much more restricted as shown by much higher Fst (0.8) for the maternally inherited mtDNA. Clark's nutcracker disperses seeds.	FSH
Pinus ponderosa Laws Two varieties: 1) *P. p.* var. *ponderosa* 2) *P. p.* var. *scopulorum* Engelm.	Ponderosa pine and Rocky Mountain ponderosa pine	Pinaceae	P	1) WR: BC and northern Rocky Mountains primarily west of the Continental divide to Pacific Coast and south to s. CA 2) northern Rocky Mountains east of the Continental Divide in MT, south to AZ, NM, NE	W, V	W	SC/M	Provenance tests, genetic diversity in different regions using allozymes, cpDNA, mtDNA, morphological differentiation of populations, interspecific and intraspecific hybridization	Rehfeldt 1990, 1991, 1993, 1999, Conkle 1973, Mitton et al. 1980, Linhart et al. 1981, Knowles & Grant 1983, Farris & Mitton, Rehfeldt et al. 1996, Latta & Mitton 1999, Sorensen 1999.	Conkle and Critchfield (1988) reviewed hybridization evidence among Ponderosae species. Ordination study in southwest by Rehfeldt et al. (1996) on morphological traits provided evidence for three varieties: *scopulorum*, *arizonica* , and *ponderosa* .	YES

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines
Pseudotsuga menziesii (Mirbel) Franco One of two varieties native to R2: 1) *P. m.* var. *glauca* (Beissn.) Franco	Douglas-fir, Rocky Mountain Douglas-fir	Pinaceae	P	1) Alberta to BC, Canada; WA e to MT, s to AZ and w TX. Also in MN and NY.	W, V	W	SC/M	Seed zones, provenance tests, breeding system variation, mating system (outcrossing rates), inbreeding, local adaptation (GxE)	Neale & Adams 1985, Campbell 1986,1991, 1992, Rehfeldt 1989, Ritland & El-Kassaby 1985, Zhang et al. 1993, Sorensen 1999	Male and female cones tend to mature at different times, promoting high outcrossing rate (Neale & Adams 1985, Copes & Sniezko 1991), but some self-pollination occurs. Most genetic work has been on var. *menziesii* (from WA, OR, CA, and NV), and on *P. m.* var. *glauca* in n Rocky Mountains. Rehfeldt (1989) summarized evidence for adaptation in var. *glauca* in n Rocky Mountain region.	YES
Trees, flower bearing											
Populus tremuloides Michaux.	Quaking aspen, trembling aspen	Salicaceae	P	WR: Labrador to AK, s to NJ, AZ, and MEX (H 1964, and M&K)	W	W	D	(See Table 10.6) Population structure, genetic diversity, clone size and diversity, hybridization	Mitton & Grant, Cheliak, Jelinski, etc.	Most common poplar in CO. Many habitats. Resembles Eurasion P. *tremula*. Dioecy enforces outcrossing. Extensive seed and pollen dispersal but no soil seed bank.	FSH
Prunus virginiana L	Common chokecherry	Rosaceae	P	Canada, s to GA, NM, and CA.	A	I	-/P	.	.	In CO at 1300-2800m.	FSH
Quercus macrocarpa Michx.	Bur oak	Fagaceae	P	WR at low elevations in se Alberta, e to Manitoba; s to TX and e to ME and AK.	W	W	-/M	Population structure, genetic diversity	Chechowitz & Chappell 1990, Schnabel & Hamrick 1990a, Geburek & Tripp-Knowles 1994	Highly outcrossing. Hybridizes with *Q. gambelii* in the w part of its distribution (Chechowitz et al. 1990) and with white oak, swamp chestnut oak, chinkapin oak, pin oak, and swamp white oak (Fowells 1965). In diverse habitats at low to mid elevations.	FSH

Species	Common name(s)	Family	Life-cycle form	General geographic range	Seed disp.	Pollen disp.	Breeding system	Types of ecological genetic studies	Reference	Additional Comments	Seed transfer guide-lines

Life-cycle form (P= perennial, B= biennial, A= annual, S= semelparous but after several years);
General geographic range (G=Geographically widespread, WR=Widespread in ecol./ environ. restricted conditions; P=Patchy distribution; R=Restricted distribution; S= Scarce, vary restricted);
Primary seed dispersal mechanism (secondary dispersal): (W= Wind; A= Avian; V= other Vertebrate; G=mainly Gravity dispersed; E= Explosive, balistic; I=Insects, generally ants);
Pollen dispersal (W= Wind; A= Avian; V= other Vertebrate; I= Insect; S= autogamous Selfer);
Breeding system --flower or cone sexual system/mode: (SC= self-compatible, SI = self-incompatible, na = not applicable / P= perfect flowers, M= monoecious, D= dioecious, G= gynodioecious, CL= some cleistogamy, DC = dichogamous, H = heterostylous, apomixis = agamospermous form where asexual seeds develop).

Table 10.2. Characteristics of some Region 2 native plant species that are known to reproduce vegetatively or resprout after disturbance. Source of information for some species on propensity for vegetative growth and type of growth structures is from FEIS (2004). Annual herbs are assumed to have no vegetative reproduction after disturbance. They rely on seeds for recruitment.

Scientific name	Common name	Organs of vegetative growth	Additional comments (extent of growth post-fire, clonal nature)	Reference
Grasses:				
Andropogon gerardii	Big bluestem	rhizomes	Clones in tallgrass prairie at Konza Prairie Biological Station, Kansas were small (1.6 plants per clone average, clone size rarely > 2 meters).	Keeler et al. 2002
Bouteloua curtipendula	Sideoats grama	rhizomes	Tillers and rhizomes can survive fire.	FEIS
Buchloe dactyloides	Buffalograss	stolons; occasionally rhizomes	Rapid vegetation spread of stolons, tillers, and rhizomes results in dense sod. Very deep root systems. Seeds enclosed in a bur tend to survive fire. Plants frequently resprout after fire from buried buds, except under high intensity fire. Sex ratio can vary among populations. Some monoecious individuals occur in the predominantely dioecious populations.	FEIS, Huff & Wu 1992
Danthonia spicata	Oatgrass, poverty grass	tussock/burried buds	1) Populations increased after fire and cutting in Michigan. About 25% survived fire. 2) Need to assess if there is apomixis in N. America	1) Scheiner 1988 2) Philipson 1985
Elymus glaucus	Blue wildrye	surface rhizome	Limited tillering. Does not appear to form clones, but this may be variable. Plants in Great Plains tend to tiller more then in northwest. Fire appears to reduce mature plants. Seeds can survive fire. Occurs in old burns and cut areas.	FEIS
Elymus lanceolatus ssp. *lanceolatus*	Thickspike wheatgrass	rhizomes	Extensive creeping rhizome system. Resprouts and generally increases after fire. Also has persistent seed bank.	FEIS
Festuca thurberi	Thurber fescue	caudex/ burried points, tufted with tillers	Marked tillering; most regeneration from seeds. Can resprout after fire and recruit with off site seeds. Some disturbance increases tillering.	FEIS

Scientific name	Common name	Organs of vegetative growth	Additional comments (extent of growth post-fire, clonal nature)	Reference
Koeleria macrantha	Prairie junegrass, crested hairgrass	tussock/burried buds	Resprouts after fire.	FEIS
Leymus triticoides	Beardless wildrye	rhizomes	Long-lived, extensive, spreading rhizome systems. In some areas, most regeneration is from rhizomes. Forms potentially large clones.	
Panicum virgatum	Switchgrass	rhizomes	Most reproduction from seeds. Bunchgrass forming ecotypes (short rhizomes) don't survive fire as will as more rhizomatous forms.	FEIS
Poa secunda	Big bluegrass, Canby bluegrass, Sandberg bluegrass	tussock/burried buds	Often summer/fall dormant where lower/dier. Frequently survives fire. Tends to form apomictic seeds (agamospermous) so populations can be highly clonal. Apomictic ovules made up 25- 100% of sample ovules in a study of 29 populations in the *P. secunda* complex from 8 states and provinces (Kellog 1987). Estimates of pollen viability tended to be lower when apomixis was higher.	FEIS, Kellogg 1987
Pseudoroegneria spicata	Bluebunch wheatgrass	tussock/burried buds	Does not spread vegetatively but usually survives fire, resprouting from protected buds.	USDA, NRCS 2004, FEIS
Herbs, subshrubs, other graminoids:				
Achillea millefolium 1) *A. m.* var. *alpicola* 2) *A. m.* var. *occidentalis*	1) Common yarrow 2) Western yarrow, wooley yarrow	rhizomes	Spreading. Extensive sprouting and rapid rhizome spread after fire, but may be killed after severe fire. Recent discovery of facultative apomixis in Eruopean forms of *Achillea millefolium* suggest apomixis should be checked in N. American populations.	FEIS, Terziiski et al. 1995, Yurukova-Grancharova et al. 2002
Antennaria rosea (all taxa)	Rosey pusseytoes	stolens and apomictic seeds	Plants spread vegetatively from stolens and apomictic seeds (highly clonal). However, not likely to survive fire.	Bayer 1990
Aquilegia caerluea	Colorado blue columbine	basal caudex	Sprouts from caudex after fire or other disturbance. Caudex, growing points in soil, no vegetative spread.	Montalvo (pers. obs.)

Scientific name	**Common name**	**Organs of vegetative growth**	**Additional comments (extent of growth post-fire, clonal nature)**	**Reference**
Artemisia ludoviciana	White sagebrush, Louisiana sagewort	rhizomes	Spreading rhizomes can form dense clones. Ability may vary with ecotype. Above ground shoots killed by fire, but have moderate resprouting ability. Reestablish quickly after disturbance from rhizomes and wind-dispersed seed.	FEIS
Balsamorhiza sagittata	Arrowleaf balsamroot	basal caudex	Resprouts from caudex after fire or other damage. Deep taproot. Can branch and form dense rosettes.	FEIS
Campanula rotundifolia	Harebell	rootstocks	Vegetative sprouts can be extensive.	Alsos et al. 2003
Carex scopulorum	Rocky Mountain sedge	rhizomes (stout horizontal rootstocks)	Study on *C. s.* var. *scopulorum* in Rocky Mountain National Park, CO, found that clones were small (not many members per clone) and that there was considerable sexual reproduction.	Linhart & Gehring 2003
Chamerion angustifolim	Fireweed	rhizomes	Extensive growth after fire. Forms clones. Increases after fire.	FEIS, Myerscough 1980
Erythronium grandiflorum	Glacier lily	corms	Often in moist sites that don't burn much. Corms resprout after fire.	FEIS
Geranium caespitosum	Geranium	rhizomes		Hessing 1988
Geranium richardsonii	Richardson's geranium	rhizomes		Harrington 1964
Geum rossii	Ross' avens	rhizomes, branched rooting caudex	Alpine turf, tight compact clones. Response to fire unknown.	Chambers 1991
Liatris punctata	Dotted gayfeather/ blazing star	rhizomes	Resprouts from rhizomes after fire. Spreads vegetatively.	FEIS
Polygonum viviparum	Alpine bistort	bulbils	In Europe, the ratio of flowers to bulbils decreased with an increase in elevation. Plants were more clonal at higher elevations. In Colorado, reproduction may be exclusively by asexual bulbils.	Diggle et al. 1998, Bauert 1993
Scutellaria brittonii	Skullcap	rhizomes	—	Harrington 1964

Scientific name	Common name	Organs of vegetative growth	Additional comments (extent of growth post-fire, clonal nature)	Reference
Sphaeralcea coccinea	Scarlet globemallow	rhizomes	Rhizomes survive fire. Disking, burning, and grazing increases scarlet globemallow production for several years. Dormant, hard seeds can build up in soil. Pioneer species.	FEIS
Shrubs:				
Amelanchier alnifolia	Saskatoon serviceberry	root crown/rhizomes	After fire or cutting, sprouts from rhizomes or root crown. Deep rooted rhizomes may survive high fire intensity.	FEIS
Arctostaphylos patula	Greenleaf manzanita	root/stem burl	Resprouts readily after fire. Seed also are stimulated to germinate by fire.	FEIS
Arctostaphylos uva-ursi	Bearberry	stem/root crown/lignotuber	Resprouts after low intensity fire. Hard seeds are likely to be stimulated to germinate by fire. Produces compact clones.	FEIS
Artemisia frigida Willd.	Fringed sagebrush	adventitious bud/root crown	Some resprouting after fire. Sometimes layers under favorable conditions.	FEIS
Ceanothus fendleri	Fendler ceanothus	adventitious bud/root crown		
Cercocarpus montanus	Mountain mahogany	adventitious bud/root crown	Resprouts vigorously from root crown after fire or other disturbance.	FEIS
Ceanothus velutinus	Snowbrush ceanothus	adventitious bud/root crown	Plants resprout from base and seed germinate from seed bank after fire.	FEIS
Chrysothamnus viscidiflorus	Low rabbitbrush, yellow rabbitbrush	adventitious bud/root crown	Plants resprout from base after cutting.	McArthur & Taylor 2004b
Quercus gambelii	Gambel oak	lignotuber/rhizomes	Top-kill of all kinds promotes vegetative sprouting. Extensive growth after fire primarily from lignotuber, while clone expansion is primarily from rhizomes. Clones several stemmed and long-lived; can form dense thickets or spaced trees.	FEIS; Tiedemann et al. 1987, Kumar & Rogstad 1998
Rhus glabra	Smooth sumac	adventitious bud/root crown	Clonal, dioecious, colonizes burns from resprouts and heat-scarified seeds.	FEIS; Chung & Waller 1986

Scientific name	Common name	Organs of vegetative growth	Additional comments (extent of growth post-fire, clonal nature)	Reference
Rhus trilobata var. *simplicifolia*	Skunkbush sumac	root crown/rhizomes	Produces long spreading rhizomes that form clones. Sprouts vigorously after fire. Can delay resprouting for a year.	FEIS
Rosa woodsii	Wood's rose	root crown/rhizomes	Sprouts from rhizomes and root crowns after low to moderate severity fire.	FEIS
Salix exigua	Sandbar willow, coyote willow	roots, root crowns	Spreads clonally and forms dense thickets. Get coppice sprouts after cutting. Seeds also colonize readily after fire.	FEIS
Salix scouleriana	Scouler willow	stump	Also known as fire willow, this plant colonizes quickly from seeds and sprouts after fire and clear cuts.	FEIS, Francis 2004
Sorbus scopulina	Mountain ash	root crown		FEIS
Sheperdia canadensis	Russet buffaloberry	roots/root crown		FEIS
Yucca baccata	Banana yucca	rhizomes		FEIS
Trees:				
Picea engelmannii	Engelmann spruce	adventitious	Layering common at upper elevations where trees are dwarfed.	Fowells 1965
Pinus albicaulis	whitbark pine	adventitious	Layering more common in krummholz forms. Has a soil seed bank which is unusual for a pine. Larger diameter trees may survive moderate intensity fire. Pioneer after fire, primarily from bird dispersed seeds.	FEIS
Populus tremuloides	Quaking aspen	roots	Extensive resprouting after fire. Also seedlings from wind dispersed seeds after fire.	Rogstead et al. 1991
Prunus virginiana	Chokecherry	root crown/rhizomes		
Quercus macrocarpa	Bur oak	adventitious	Sprouts vigorously after fire from base.	Fowells 1965

Table 10.3. Information on local adaptation or genetic differentiation in sample of plant species native to at least one of the five states in Forest Service Region 2.

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Grasses:				
Andropogon gerardii	Big bluestem	1) R (KS, IL) 2) R (AR, IL) 3) R (KS, IL)	1) In a reciprocal experiment (plants, soil, and mycorrhizal fungi), there were significant differences in growth of plants in response to colonization by local and non-local fungi and soil environment. Each population grew better in its home soil, in part due to differences in local fungi, indicating local adaptation to soil environments. 2) RAPD analysis of remnant prairie populations showed 82.7 to 99.3% of variation within and 11% among populations. IL prairie and cultivar populations differed from AR populations. Isolated populations were genetically variable, and relationships among populations could not be predicted solely on proximity of sample locations. 3) In a greenhouse competition study, cultivars ‘Rountree’ and 'Pawnee' were larger than local and non-local plants regardless of competitor density and identity. In the field, non-local plants were significantly smaller than local plants and cultivars. Provenance and cultivar selection history significantly influenced competitive ability. The higher competitive ability of the cultivars suggests they can out compete and potentially swamp local populations. Highly competitive cultivars could be deleterious to natural ecosystems.	1) Schultz et al. 2001 2) Gustafson et al. 1999 3) Gustafson et al. 2004a,b
Bromus carinatus	California brome	1) R (central CA, AZ)	1) Individuals differ in degree of cleistogamy and plants are facultatively chasmogamous. Environment found to affect proportion of cleistogamous flowers. Strong differentiation among populations in timing of flowering, stature, and in degree of facultative chasmogamy. Planted 232 maternal families of seeds from different geographic areas (from AZ and central CA) in common garden. Plants within families were generally uniform (indicating homozygosity). There was morphological variation among families of plants within geographic groups. Results indicated much self-pollination (from facultative cleistogamous flowers). This would lead to homozygosity and swarms of local races. Then hybridization among races may occasionally occur, creating heterozygotes. Subsequent selfing increases homozygosity.	1) Harlan 1945a,b

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Buchloe dactyloides	Buffalograss	1) R (TX, MEX) 2) R (TX, CO, NM, KS, OK) 3) R (AZ, NE, OK, CO, TX-- all are germplasm accession locations)	1) Studied variation in rare diploid populations from MEX and TX for RAPD and allozyme variation. RAPDs showed "greater variation among regions (58.4% of total variance) than allozymes (45.2%), but less variation among individuals within populations (31.9% for RAPDs vs. 45.2% for allozymes); the proportion of genetic variance among populations within regions was similar (9.7% for RAPDs vs. 9.6% for allozymes)." 2) 242 wild populations of the southern Great Plains are differentiated as 2x, 4x, 5x, or 6x, with hexaploids making up 73% of collections, followed by 22% tetraploids, and < 3% diploids and pentaploids. Higher ploidy levels were associated with higher precipitation, but no clear geographic pattern was detected. 3) Examined 53 germplasms (included germplasm releases and cultivars) for molecular marker variation (SRAP) and ploidy level. Eight clusters of populations were detected, and groups tended to be associated with ploidy. Overall heterozygosity was high (He= 0.35). Significant genetic differentiation was indicated by the SRAP and ploidy differences.	1) Peakall et al. 1995 2) Johnson et al. 2001 3) Budak et al. 2004
Bouteloua curtipendula	Sideoats grama	1) R/G (ND, OK, TX) 2) R (southern Manitoba, Canada ; 30 km apart) 3) R (Manitoba, and releases from ND, SD, MN)	1) Clonal divisions of plants from TX, OK, and ND were grown in a greenhouse at 13, 14, 15 hour daylengths and natural Chicago daylength from April to November. Significant differences in flowering time and success occurred among strains. The TX strains flowered fastest and best at 13 hr, few flowered at 15, and none at 15hr. The mid-latitude OK strain flowered at 13 and 14 hr. The northern ND strains flowered vigorously at 14, 15, and natural daylength. this pattern of flowering was consistent with a population x environment interaction and is evidence for differences in adaptation to daylength. 2) RAPD analysis of 11 populations (see Table 8.2). No isolation by distance detected. 97.8 of variation was within populations, and 2.2% among. The among population variation was very low, and suggested high gene flow. 3) AFLP variation of same 11 populations (Table 8.2). Compared band frequencies of accessions (under development) and cultivars. There were small, but significant genetic shifts. AFLP band variation was high.	1) Olmstead 1945 2) Phan et al. 2003 3) Fu et al. 2004
Bouteloua gracilis	Blue grama	1) G (Canada to sw. US, including AZ, KS, IA, WY, NE, CO, NM) 3) G (AZ, KS, WY, NE, CO, NM, TX, ND) 2) R (Manitoba)	1) In common environment study found population differentiation in flowering time, tillering, cytotype. Timing of flowering is often adaptive. 2) 9 populations grown for 2 years; many differences among populations. 3) For 11 natural populations separated by > 30 km, band frequency for each population averaged 0.42. Ninety-seven percent of total RAPD variation was found within natural populations, with 3 percent among populations.	1) Fults 1942 2) Riegel 1940 3) Phan et al. 2003

Scientific name	**Common name**	**Scale of genetic information available***	**Genetic information (if more than one study, ordered as in "scale" column)**	**Reference**
Danthonia spicata	Oatgrass	1) R (MI) 2) R (NC)	1) Quantitative genetics study of 5 local populations from range of seral stages. Plants were cloned and grown in multiple common greenhouse environments (varied moisture and light). 40% to 90% of phenotypic variation was plastic. Populations differed significantly in time to flower and in a range of other traits, but plasticity was much stronger. Plants occupied local area environmental gradient and were phenotypically flexible. Plasticity did not differ among populations. 2) Variation exists among populations in degree of cleistogamy and outcrossing. Broad sense heritability for inflorescence traits was detected in common garden using clones.	1) Schiener & Goodnight 1984 2) Clay 1983, Clay & Antonovics 1985
Elymus elymoides (=Sitanion hystrix)	Bottlebrush squirreltail	1) R (AZ, CO, NE, NV, NM, SD, UT) 2) G 3) R (Intermountain Region-- NV, ID, tested plant materials)	1) Twelve collections from seven states and elevations ranging from 1380 - 2980 m were planted in a common garden near Flagstaff AZ and in a growth chamber. Populations differed in phenology. Phenology could be predicted by temperature and moisture conditions of home sites suggesting adaptation to climatic factors. Flowering dates differed by as much as two months. 2) 27 accessions from multiple states were evaluated for ecological and physiological traits with respect to geographical origin. Subspecific taxa were successfully distinguished statistically by habitat and geography. Timing of growth and maturation and size varied. Evidence for ecotypic differences was strong. Authors suggest matching restoration site with genetically and ecologically appropriate material. 3) Seed accessions differed significantly.	1) Clary 1975 2) Jones et al. 2003 3) Young et al. 2003
Elymus glaucus ssp. *glaucus* and *E. g.* ssp. *jepsonii* (possibly also *E. g.* ssp. *virescens*)	Blue wildrye	1) R (CA Sierra Nevada) 2) R (WA, OR, CA) 3) R (OR, CA) 4) R (OR) 5) R (CA)	1) Populations from along a 75 mi long elevation gradient in CA were grown together in lathhouse at low elevation. High elevation populations were shorter and flowered 4-8 wk later than those from low elevation. 2) & 3) Two separate allozyme studies indicated low H_e (0.19 and 0.03) and a deficit of heterozygotes, but a high level of polymorphic loci (80 and 77%) in this allotetraploid. High levels of population differentiation were consistent with an inbred mating system and low levels of gene flow among populations (20 populations, Fst = 0.549; 133 populations, Fst = 0.40, study 2 and 3 respectively). 4) A common garden study of 78 sources if *E. g.* ssp *jepsonii* and 75 sources of *E. g.* ssp. *glaucus* revealed a strong relationship between environment of seed source and quantitative traits. Results were consistent with adaptive differences among populations. Seed transfer guidelines were provided for area of study. 5) Evidence for local adaptation *These studies provide evidence that translocations deserve careful planning to avoid maladaptation and potential outbreeding derpression.*	1) Snyder 1950 2) Knapp & Rice 1996 3) Wilson et al. 2001 4) Erickson et al. 2004 5) Hufford & Mazer pers com.

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Festuca arizonica	Arizona fescue	1) R (CO)	1) Allozyme study of a single PGI locus for three populations from Gunnison Basin, CO indicated an excess of heterozygous genotypes. They found significant differences in allele frequencies among populations but did not detect a significant Fst. There were 8 alleles detected at the PGI locus. More populations and loci need to be studied, but these initial results are consistent with a high level of outcrossing and gene flow.	1) Pentergast et al. 2004
Festuca thurberi	Thurber fescue	1) R (CO)	1) Six populations were assayed for two PGI loci (allozyme study) across an elevational gradient. Average H_e was high (= 0.51) and Fst was very low (=0.0068),values consistent with high levels of gene flow and outcrossing.	1) Pentergast et al. 2004
Koeleria macrantha (Ledeb.) J. A. Schultes (= *K. cristata* auct. p.p. non Pers., *K. gracilis* Pers., *Koeleria nitida* Nutt.)	Prairie junegrass, crested hairgrass	1) R (CO, KS, SD) 2) R (Sask. Canada; CO, ND, MT, NM)	1) Grew plants in common garden at Lincoln< NE. Northern and western areas where rainfall is low, showed that plants with early phenology and short stature were those from areas with short growing season and early phenology (growth). 2) "Transplant" common garden. Selected most vigorous plants from previous garden to establish new garden. These results contrasted with previous studies in that the plants from highest population were latest to develop. Precipitation of source habitat had the largest association with phenology and morphology. The growth curves also varied among the different populations. These studies provide evidence for population differentiation and the presence of adaptive differences in either growth or morphology that may vary among regions.	1) McMillan 1959 2)Robertson & Ward 1970
Panicum virgatum	Switchgrass	1) R (synthetic population from 3 cultivars) 2) R (MN, SD, NE, IA, IL, MO) 3) R(IL SD, IA- and cultivars) 4) G (TX to SD)	Lowland ecotypes are tetraploids and most upland plants are octoploid. 1) Eleven lowland populations were evaluated and significant differences were found among half-sib families. Tiller number correlated with yield. Enough variation was detected to allow breeding. 2) Mode of inheritance of cpDNA was primarily maternally inherited. For all traits measured, except seed width, hybrids were intermediate to parents . 3) Found much G x E in evaluation of 23 populations were important for all traits. Also found postfertilization incompatibility system that prohibits successful mating between hexaploids and octoploid. 4) In common garden test, found differences among 20 populations. Cytotype (upland vs lowland) explained much of the variation among populations and the population x location interaction, and ecotypic differentiation explained a lot of variation in adaptation. Much latitudinal variation/adaptation.	1) Das et al. 2004 2) Hopkins et al. 1995, 3) Martinez-Reyna 2002 4) Casler et al. 2004

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Poa alpina	Alpine bluegrass	R (Alberta)	There were significant differences in seed mass and germination percentages among different seed accessions (provenances). There were even stronger effects of maternal environment. Apomictic seeds and pieces of 10 tussocks from two sites near Jasper Alberta (1800m and 2030 m elevation) were collected. Tussocks were grown in nursery to produce seeds to compare with wild-collected seeds. Seeds from 6 different accessions were also planted in common nursery environment and seeds harvested to produced reclamation lines. Seeds from nursery plots germinated faster and at higher percentage than wild-collected seeds.	Hermesh & Acharya 1992
Poa secunda	Sandberg bluegrass, Canby bluegrass, big bluegrass	1& 2) G 3) R (WA, OR, WY, Yukon, ID)	1) Much data from common gardens. Over species range, continuous variation in vegetative and floral structures. There is, however, high among population differentiation, likely due to combination of mixed mating and apomixis. Occupies diverse soils and elevations (0 to 4000 m). Phenology varies from April, May or June, vs. July or August and correlates with elevation of origin and growing season. 2) Common gardens at multiples sites with intra- and inter-specific F1 and F2 hybrids. Apomixis complicated study. Big morphological differences among populations. 3) Study of variation in two natural populations and two cultivars (see Table 8.2) using AFLP banding patterns (due to high polyploidy). 'Sherman' has a single genotype and 'Canbar' has three genotypes-- shows severe genetic erosion and/or original collections from few genotypes. Two natural populations more diverse but similar to each other suggesting high gene flow, but perhaps artifact of scoring banding patterns. Ample opportunity for local adaptation.	1) Kellogg 1985, 1990 2) Hiesey & Nobs 1982 3) Larson et al. 2001
Pseudoroegneria spicata	Bluebunch wheatgrass	1) multiple R (WA, OR, ID, BC, AB, MT, NV, UT, WY, CO) 2) multiple R (WA, OR, ID, MT, NV, UT, WY, CO)	1) Large study with DNA (AFLP) marker variation examined 565 plants from 82 (5-7 plants/location) over much of species distribution; 81locations (source sites) were single-origin accessions, one was 'P-7' (multiple origin cultivar), and one was unknown (note: CO represented by two locations, WY by 3; ND and SD not sampled). 18.3% of the variation was partitioned among 21 groups identified by the analysis, 14.9% was due to among localities within groups, and 66.8% of the variation within locations. Although there was a pattern consistent with isolation by distance (genetic distance was correlated with geographic distance), population differentiation into regional groups was significant. Two CO pops were distinct from other pops, but one CO population clustered with two WY populations. 2) Seeds from 47 natural populations and 'Goldar' (see Chapter 8) for germination, growth, seed wt. Significant differences in seed wt and germination rate at optimum 15/25 ^{o}C and cold (1 ^{o}C) observed. Mean shoot wt at 28 days varied among accessions by factor of 6.	1) Larson et al. 2004 2) Kitchen & Monsen 1994

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Herbs, other graminoids, subshrubs:				
Achillea millefolium *A. m.* var. *alpicola* *A. m.* var. *occidentalis*	Western yarrow (wooley yarrow)	1) G (gardens in CA) 2) R (CA) 3) R (MT, Canada (BC, AB, Sask))	1) For *A. millefolium* complex, striking differences in stature from different elevations were retained in common gardens and shown to be heritable. Some evidence for local adaptation of contrasting ecological races to particular elevations/sites. 2) *A. lanulosa* (now *A. m*. var. *occidentalis*) plants from contrasting elevations (1400 m and 3050 m) were strongly genetically differentiated for carbon assimilation rate (~photosynthetic rate) suggesting physiological adaptation to altitude. 3) Allozyme study of two tetraploid subspecies (13 and 6 populations) revealed He= 0.126 and 0.085; Gst= 0.300 and 0.078, showing substantial differences in population substructuring and heterozygosity between subspecies. Gene flow was higher in subspecies from Canadian sand dune. 4) Recommend planting locally adapted ecotypes in appropriate locations.	1) Clausen, Keck, & Hiesey 1940; Hiesey & Nobs 1970 2) Gurevitch 1992 3) Purdy & Bayer 1995 4) Monsen et al. 2004
Antennaria rosa 1) *A. r.* ssp. *rosea* 2) *A. r.* ssp. *arida* 3) *A. r.* ssp. *confinis* 4) *A. r.* ssp. *pulvinata*	Rosy pussytoes	R (western end of species range: AK, BC, MT, WY, CO, WY, OR, ID, CA, NV, AZ, NM)	Allozyme study of tetraploid and triploid populations of *A. rosea* complex examined clonal diversity in this mixed sexual and apomictic species (facultative apomict). Scired alleles at 4 polymorphic loci. Populations averaged 3.5 clones, and 27% had a single clone. Genotypes tended to be unique or to occur in few localized populations. There was no relationship between clone diversity and elevation, latitude, or longitude. Populations in areas with higher numbers of other sexual species of *Antennaria* (possible relatives) had higher clonal diversity, suggesting hybridization with other species in those areas. Populations in areas that were glaciated during the Pliestocene had fewer clones than areas that weren't glaciated.	Bayer 1989, 1990
Aquilegia caerulea 1) *A. c.* var. *alpina* 2) *A. c.* var. *caerulea* 3) *A. c.* var. *daileyae* 4) *A. c.* var. *ochroleuca* 5) *A. c.* var. *pinetorum*	Blue columbine, Colorado blue columbine	2) R (AZ, CO, NM, WY) 3) R (AZ, CO, UT)	Geographic patterns in flower color and spur length are strong, resulting in five varieties. 1) Flower color and spur length are genetically determined, but spur length is also modified by environment. 2) Geographic pattern in spur length correlates with tongue lengths of pollinating hawkmoths suggesting traits coevolved and improved pollen deposition/seed production and pollinator fitness. Bumblebees favor blue flowers and hawkmoths favor white flowers. In the sw where hawkmoths are more frequent, flowers are pale blue to white with long spurs. 3) Outcrossing rate correlates with differences in flower morphology; white end of range more outcrossed. 4) For closely related species in AZ, TX, and MEX, a study of cpDNA found little evidence for gene flow among populations due to seed dispersal. Gallagher (2003), however, found evidence for ample gene flow among populations from pollen dispersal (based on DNA techniques). *Translocating outside home range of a variety could lead to floral trait mismatches with pollinators and lower reproductive success.*	1) Prazmo 1965 2) Miller 1981 3) Brunet and Sweet 2004 4) Strand et al. 1996, Gallagher 2003

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Balsamorhiza sagittata	Arrowleaf balsamroot	R (Intermountain Region)	This species grows in a variety of precipitation zones and in many soil types. Plant populations vary with respect to drought tolerance and palatability. Ecotypes are likely and appear to influence success of seeding. Monsen et al. 2004 recommend using seeds from sites similar to area proposed for planting.	Monsen et al. 2004
Campanula americana	American bellflower	1) G (MI, KT, GA, FL) 2) R (VA)	1) Seeds collected from latitudinal gradient across range of species. Greenhouse study of 5 populations showed significant population differentiation in numerous phenological and morphological traits and annual vs biennial life history. Much larger variation among populations than within populations for timing of seed germination. 2) Pollen color varies from tan to purple and populations differ in frequency of the different colors. Depending on local pollinator fauna, this could affect seed production. Halictid bees visit tan pollen flowers preferentially. They also over visit flowers in male phase which decreases pollinator efficiency relative to bumblebee pollinators that don't discriminate. The particular composition of pollinator groups and flower colors can have varying effects on seed production. 3) Experimental study detected significant maternal and paternal effects on seed mass, timing of germination, and amount of germination. Timing of seed germination influenced if the resulting plant was annual or biennial. There was broad sense heritability for life-history and significant differences among populatic	1) Kalisz & Wardle 1994 2) Lau & Galloway 2004 3) Galloway 2001 a, b
Carex scopulorum 1) *C. s.* var. *scopulorum* 2) *C. s.* var. *bracteosa* 3) *C. s.* var. *pruinophylla*	Rocky Mountain sedge	L (Rocky Mountain National Park, CO)	Clones studied in diverse microenvironments (moist to wet to very wet) at elevation 3800 - 3950 m. Clones small; no relationship between genetic and geographic distance (i.e., neighboring clones not necessarily more genetically similar than more distant clones). Results suggest significant cross-pollination and establishment by seeds. Significant differences in alcohol deyhdrogenase (ADH) allele frequencies between populations occupying wet vs. moist sites. Because ADH enzyme affects metabolism under oxgen-limiting conditions, this suggests there could be adaptive differences. The three varieties grow in similar habitat but primarily at different elevations. In R2, *C. s. s.* occurs from 3000-4500 , while *C. s. b.* occurs from primarily from 1200-3000 ft. This suggests there may be adaptive differences.	Linhart & Gehring 2003; Flora of North America

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Chamaecrista fasciculata	Partridge pea	1) R (MD, IL) 2 & 3) R (KS, OK, MN)	1) Reciprocal transplant study with two populations showed differences among populations in fitness traits but only weakly significant local adaptation in one of two years. 2) Reciprocal transplant study showed significant home site advantage with reductions in seed production at foreign sites. This study showed there was heritable variation and that there was a response to selection upon moving plants to different habitats. Studies show maladaptation when translocate to other sites for the species across climatic gradient. 3) Offspring of controlled crosses were planted in common gardens across a climatic gradient. In each garden, native populations produced significantly more seeds showing substantial home site advantage. Heritable quantitative genetic variation was higher in native locations and in the more southern populations. The study suggests that as climate gets warmer, that the northern population would be less able to respond to selection than the southern populations.	1) Galloway & Fenster 1999; 2) Etterson & Shaw 2001 3) Etterson 2004a,b
Chamerion angustifolium	Fire weed	R (MT, WY)	Most populations are either diploid or tetraploid. Flowers of diploids have shorter petals and styles and shorter inflorescences than tetraploids. Flowering periods overlap by 51%. Pollinators tend to be true to cytotypes: only 15% of flights were between cytotypes. The combination of flowering asynchrony and lower pollinator movement among cytotypes helps to limit hybridization and reduce potential outbreeding depression. Still, 6.6% of pollinations were between cytotypes. *This suggests only using dominant cytotype at a site.*	Husband & Schemske 2000
Collomia linearis	Collomia	L (AK to QU, s to MN, CO, AZ and CA)	Qst for corolla traits and time to flower was larger among than within populations. Such differences in maturation time and floral traits are often adaptive.	Wilken 1977
Dalea purpurea	Purple prairie clover	R (KS, IL)	Using molecular markers, found low population divergence among prairie remnants (Fst = 0.042), and correlation between geographic and genetic distance. RAPD and allozyme markers showed 86% and 77% of variation within populations, respectively. There were significant differences between a Konza Prairie population and Illionis populations. In greenhouse experiment, there were differences among populations in competitive ability (between cultivar and wild populations) that was not associated with genetic diversity. Cultivars were superior competitors suggesting their use could disrupt local communities.	Gustafsen et al. 2002

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Delphinium nuttallianum (=D. nelsonii)	Nelson's larkspur	L (CO), 3 km	1) Genetic variation in flower color (white and pale mutants), with light colored mutants discriminated against by bumblebee and hummingbird pollinators. 2) Six populations separated by up to 3 km were assessed for allozyme variation. At this small spatial scale, litle population differentiation was detected (Fst ranged 0.0005-0.05) indicating plenty of gene flow has occurred in the area over time. No isolation by distance was detected. 3) Pollen dispersal can occur between plants separated by 100s of meters. Documented pollen deposition on plants 400 m from pollen source. Suggests isolated populations in mountains are part of meta-population.	1)Waser & 1981 2) Williams & Waser 1999 3) Schulke & Waser 2001
Gaillardia pulchella	Blanket flower, fire-wheel	R (TX, NM)	Allozyme study of 54 populations over large geographic area. Gst = 0.160 among populations of the same variety and 0.021 between varieties. There was a significant pattern of isolation by distance suggesting that high gene flow could deterrent population differentiation.	Heywood & Levin 1984
Geranium caespitosum	James geranium	L (CO)	Common garden with plants from elevational range in CO. Variation in floral morphology was limited but variation in gynodioecy, sexual specialization, and pollen sterility was observed in high elevation populations. Expect these differences to affect mating system and reproductive success in different environments.	Hessing 1989b
Helianthus annuus	Sunflower	R (Great Plains, western USA, Mexico, and various cultivars)	Plants from Great Plains were genetically differentiated from those from California and SW (Mexico, Arizona, Texas, New Mexico)	Cronn et al. 1997
Impatiens capensis	Jewelweed	1) R (WI, MA, RI, NJ) 2) R (RI) 3) R (WI)	1) 26% of isozyme loci were polymorphic, He = 0.039 was low, total average inbreeding coefficient = 0.57, Fst = 0.46 indicating low gene flow and substantial structure. 2) Planted seeds from selfed (cleistogamous flowers) and outcrossed chasmogamous flowers in the field at different distances from mother plant. Inbreeding depression increased with distance from mother plant suggesting local adaptation to microsite of mother. 3) Quantitative genetic study of 16 life-history and morphological traits for two populations revealed positive genetic correlations between components of fitness. One of the populations revealed significant narrow sense heritabilities for several traits, including dry biomass, an indicator of plant size and fecundity. Seed mass had a large influence of mother.	1) Knight & Waller 1987 2) Schmitt & Gamble 1990 3) Mitchell-Olds 1986

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Ipomopsis aggregatta	Scarlet gilia	1) L (AZ) 2) G (ID, MT, UT, CO, CA, WY, OR, NM) 3) L (CO) 4) R (CO, AZ)	1) Plants that shift to lighter color through season produce more seeds than plants that don't shift. Hummingbirds visit plants early in season.and are replaced by hawkmoths that arrive late in season and prefer lighter flowers. 2) In allozyme study of 8 subspecies and two related species, estimates of gene flow among geographic races were relatively high (Nm>1), as were estimates of gene flow with *I. tenuituba* . 3) Study provided evidence that pollinating hummingbirds select for floral traits that differ significantly from those possessed by *I. tenuituba* . 4) Review describes experimental evidence for influence of pollinator type on evolution of floral traits and presence of geographic variation in pollinator preferences. Both the physical environment and pollinators select on the complex variation in traits observed in scarlet gilia, the related *I. tenuituba* , and hybrids between these species.	1) Paige & Whitham 1985 2) Wolf & Soltis 1992 3) Campbell et al. 1997 4) Campbell 2004
Linum lewisii	Lewis blue flax (Lewis flax, blue flax)	1) R (Intermountain region: UT, ID, NV, and WA)	1) Significant broad-sense heritability in seed dormancy, rust resistance, and survival in common gardens. Seed sources vary in dormancy and response to pre-chill. High elevation populations emerge in spring and have little carryover of seed. Low elevation populations with less predicable precipitation were more dormant.	1) Meyer & Kitchen 1994, 1995, Kichen 1994
Lobelia siphilitica L.	Great blue lobelia	1, 2) R (IA)	Nuclear-cytoplasmic gynodioecy is genetically controlled breeding system. Gender of plants is likely influenced by a combination of male sterility genes and a nuclear gene that restores male fertility. 1) From two populations of plants in the greenhouse, produced progeny of know parentage for quantitative genetics study. Female plants had smaller flowers and more exerted stigmas than gynodioecious plants. Physiological traits (e.g., photosynthetic rate, stomatal conductance, water-use efficiency) and floral morphology differed among populations and mating types. Several cross-gender genetic correlations were significant. 2) Quantitative genetic analysis of greenhouse grown progeny from two populations showed significant genetic variation for seven floral traits, including measures of flower size and number. There was a negative genetic correlation for flower number and four measures of flower size and additional evidence for a tradeoff that constrains the evolution of floral display size.	1) Caruso et al. 2003 2) Caruso 2004

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Mimulus guttatus	Common yellow monkeyflower, seep monkeyflower	1) L (CA) 2) R (CA) 3) R (CA) 4) R (CA) 5) G (s BC to MEX through OR, WA, CA) 6) R (CA) 7) R (UT) 8) R (OR)	1) Pollen from metal tolerant genotypes sire 24% more seeds in maternal parents growing in heavy metal (copper) environment than pollen from non-tolerant males. 2) Copper tolerance controlled by variation at a single major gene and therefore subject to selection and rapid evolution. Capable of very local adaptation to heavy metal soils. Variation in life-history-- annual vs perennial. 3) Some populations are facultative perennials and others are obligate annuals. 4, 5) Much genetic variation in floral traits. Small flowered populations are selfing and called *M. nasutus* and *M. micranthus* . Traits correlate with mating system. 6) Herbivory by spittlebugs is more dramatic on inbred plants. Genetic variation in tolerance to herbivory was detected. 7) Morphological variation observed among populations separated by physical barriers in Utah. Pollen and seed dispersal examined in relation to crossing barries. 7) Hybridization and introgression of *M. nasutus* into *M. guttatus* adds to genetic variation in areas of species overlap.	1) Searcy & Macnair 1990 2) Macnair 1983 3) Vickery 1958 4) Dudash & Carr 1998 5) Swiegart & Willis 2003 6) Ivey et al. 2004 7) Waser et al. 1982 8) Fishman et al. 2002
Mimulus lewisii	Purple monkeyflower	1) G (CA, UT, WA, MT, NV)	1) Common gardens with many populations planted at multiple locations in CA provided evidence of genetic differentiation in physiological traits with respect to habitat, especially temperature. Establishment of seedlings varied considerably among populations in different habitats. In addition, in comparisons with *M. cardinalis* , each parent had an advantage in its home environment suggesting local adaptation on a species basis.	1) Hiesey & Nobs 1971
Polemonium viscosum	Alpine skypilot	L (CO)	1) Populations show continuous differentiation in flower size and fragrance that differ in response to herbivory, drought, and pollinator use. Pollinators select for broader and deeper flowers because they preferentially visit larger flowers and cause more seed production. In contrast, ants prefer wider flowers and select for smaller, narrower flowers because they damage flowers when they thieve nectar, causing decreased seed production. Large flowers need more water than small flowered forms, and this selects against larger flowers at higher elevations, but ants are absent at higher elevation. Sweet-flowered plants are visited more often by bees and ants. Skunky scented plants occur at lower sites and are visited more by flies. 2) Fst = 0.015 and 0.069 was significant for populations separated by 1.5 km and 1,500 m elevation suggesting limited gene dispersal between sweet and skunky-scented populations. Reciprocal transplants between the sites showed significant home site advantage (local adaptation). *Populations are locally adapted to both the biological and physical environment at different elevations in the Rocky Mountains.*	1) Galen & Kevan 1980, Galen 1989, 1999, 2000. Galen et al. 1999, 2) Galen et al. 1991

Scientific name	**Common name**	**Scale of genetic information available***	**Genetic information (if more than one study, ordered as in "scale" column)**	**Reference**
Polygonum viviparum	Alpine bistort	1) R (Europe, Alps) 2) R (CO)	1) Little or no genetic variation was detected in lowland Alps populations and most genotypes only occurred in one population. Swiss Alps populations ranged from 450 m to 2530 m. Flowers were replaced by bulbils at higher ratios as elevation increased, suggesting either adaptation to cold or lack of induction of flowering at high elevation. 2) Intensive sampling of populations from three different communities of alpine tundra in the Front Range of Colorado showed that they differed in clonal diversity and size of clones. Allozyme analysis of this high polypoid revealed three polymorphic loci. Eleven banding phenotypes (genotypes) were detected pooling over all three populations and conservatively identified clones. The wet meadow had more genotypes than the dry meadow and fell-filed populations. 68%-72% of plants were part of a clone. Most clones had < 10 ramets and some were at all three sites.	1) Bauert 1993, 1996 2) Diggle et al. 1998
Scutellaria brittonii	Skullcap	R (WY, CO)	$F_{ST} = 0.208$ based on allozyme study of three populations. These patchily distributed, self-compatible populations of pondrosa pine forests are significantly differentiated.	Olmstead 1990
Sphaeralcea coccinea	Scarlet globemallow	G (CA, AZ, CO, ED, NV, UT, and WY)	Seeds from 37 accessions of *Sphaeralcea* (four species) were germinated in greenhouse, later transplanted into common gardens at Logan UT and Curlew Valley, ID, and monitored for at least three years. Survival was high in both gardens but lower at ID and did not differ among accessions. Stem number and weight differed among accessions; flowering time and seed production differed among garden locations. There were also differnces in rhizome growth among accessions. *These results, together with subspecific classification, indicate there is significant genetic differentiation in morphology. The differences in survival and growth between common gardens indicate potential differences in adaptation.*	Pendery & Rumbaugh 1990
Stanleya pinnata	Prince's plume, desert plume	R (CA, CO, MT, ND, NV, UT, WY)	Sixteen populations from transect from s. CA to ND grown in glasshouse from seeds. Found significant variation in selenium accumulation among populations.	Feist & Parker 2001
Trillium grandiflorum and *T. erectum*	White trillium	G (eastern North America- different species in Region 2)	Isolation by distance, genetic diversity including population structure, effect of crossing distance (0-1500 m), outcrossing rates,	Irwin 2001

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Shrubs:				
Artemisia tridentata 1) *A. t.* ssp. *tridentata* 2) *A. t.* ssp. *vaseyana* 3) *A. t.* ssp. *wyomingensis* 4) *A. t.* ssp. *spiciformis*	1) Basin big sagebrush 2) Mountain big sagebrush 3) Wyoming big sagebrush 4) Big sagebrush	1) R (CO, NV, UT, WY) 2) G & R (CO, NV, UT, WY) 3, 4, 5) R/L (UT)	1) Seedling growth of three subspecies (seeds from 4-5 populations each) in common greenhouse environment for 6 mo differed significantly. Subspecies *wyomingensis* peaked in growth rate 2 wk earlier than others. 2) In common garden study with 15 source populations, found habitat correlated patterns in seed germination and effect of chilling (genetic basis not determined). Seed germination response to chill was correlated with mean January temperature of collection site all subspecies. 3) Subspecies adapted to different site conditions, intervarietal hybrid adapted to ecotone between parental habitats. 4) Subspecies and hybrids differed in absorption of elements. Local adaptation (G x E) was found in uptake of several elements. 5) Reciprocal translplant study of seedlings and soil suggested that the microorganisms with which the plants interact may be adapted to native soil, and that the plants in turn, may be adapted to native microorganisms. *Date strongly suggest that seed transfer occur only within areas of subspecies distributions and zones of adaptation as stated in seed transfer guidelines.*	1) Booth et al. 1990 2) Meyer et al. 1990, Meyer & Monsen 1990, 1991, 1992 3) Graham et al. 1995 4) Wang et al. 1997, 1999 5) Miglia et al. 2004
Atriplex canescens	Fourwind saltbush	1) G 2) R (UT) 3) R (UT, NV, AZ, NM, CO)	1) Large adaptive differences have been discovered from planting failures and from common gardens. 2) Populations vary in sexual system. Diploids are usually dioecious and the more common tetraploid populations vary in being dioecious or monoecious. Common garden studies revealed differences in vegetative growth among sexual types. 3) Seventeen accessions were planted in common garden at two mid elevation sites in UT. Significant differences were observed among accessions in height, growth form, and disease resistance. There was significant GxE in most traits measured. Also presented literature review table of differences among sites or accessions for numerous traits, including soil traits, stem rooting, protein, seed production and germination, palatability, sex expression, chromosome number, growth rate and form. *The substantial differences in fitness related traits (reproduction, disease resistance, survival, growth rate) support having careful seed transfer guidelines. See seed transfer guidelines for this species.*	1) Sanderson et al. 2004 2) Pendleton et al. 1992 3) McArthur et al. 1983

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Chrysothamnus viscidiflorus	Low rabbitbrush	R (Intermountain Region)	Germination rates can vary widely between subspecies under different conditions. Plants from higher elevations have higher seed dormancy than those from lower elevations. Different cytotypes within subspecies are adapted to different environments (elevation and moisture patterns), and different subspecies tend to occur at different elevations. *All these patterns suggest translocation to different habitats would be maladaptive.*	McArthur & Taylor 2004b
Ericameria nauseosa (=*Chrysothamnus nauseosus*)	Rubber rabbitbrush	1) R (AZ, CA, UT) 2) R (Intermountain Region)	1) Habitat correlated patterns in seed dormancy and germination in lab. 2) Seed accessions from three vegetation types (and three subspecies) were planted in field plots. Seedling establishment was related to site of origin and consistent with adaptive pattern observed in lab studies. *Avoid translocating to maladapted seed germination environment.*	1) Meyer et al. 1989 2) Meyer & Monsen 1990
Purshia tridentata	Antelope bitterbrush	R (UT)	Examined seeds from plants from 3 accessions (and crosses between them) growing in a common garden in UT. Bulk seed collections from native sites showed differences in dormancy, but in the common garden there was more variation within than among populations. Seed dormancy differed among ovule parents in each of two years examined. Seeds from crosses of parents with contrasting dormancy showed there are effects due to environment of ovule parent, but most control involves both parents. There was also variation at the level of excised embryos, but the testa had overiding effects. Together, this showed that the seed coat (which is diploid maternal tissue), and the genotype of the embryo both affect seed dormancy. Such genetic effects on seed dormancy may be subject to selection.	Meyer & Pendleton 2000
Quercus gambelii	Gambel oak	1) R (CO, UT) 2) R (CO)	1) This study did not report sampling methods or if repeated sampling of individual clones occurred. Population structure based on allozyme samples was low (Gst = 0.119) and genetic diversity within populations was high (He = 0.204). High levels of gene flow were estimated from rare alleles (more than 7 migrants/generation). 2) This study identified clones and sampled individual clones (genets) once. Fst for genets = 0.023, He = 0.796, with clonal clumps ranging mostly from 1-20 m in diameter .	1) Schnabel & Hamrick 1990a 2) Kumar & Rogstad 1998
Rhus glabra	Smooth sumac	R (GA, VI, NC, OK)	Six populations from midwest to eastern US examined for genetic diversity: He=0.14, Gst=0.198 showing intermediate levels of variation within populations and significant population differentiation. Species level P=88%, and A= 2.3. Genetic similarities ranged from 0.83-0.99 with a mean of 0.93. This is a rather high similarity for such widely spaced populations.	Sherman-Broyles et al. 1992

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Trees:				
Abies concolor	White fir	1) L (CO)	1) Most white fir have green cones, but in CO and NM, there is a polymorphism in cone color (green vs purple). The frequency of purple coned plants increased with elevation in CO along two long transects. 2) For wild-collected cones (not from common garden), seed mass decreased significantly with elevation, but the association differed between locations and years and elevation had a stronger effect on seed mass than cone color.	1) Sturgeon & Mitton 1980 2) Farris & Mitton 1985
Picea engelmannii	Engelmann spruce	1) R (ID, MT, WY, NV, UT, CO, NM, AZ)	1) Common garden studies in Idaho with 104 Intermountain West populations. There were genetic differences among populations for 16 traits. Multiple regression showed gentle clines and accounted for 70% of the phenotypic variance among populations. Elevation and latitude were important factors. Minimum distance in elevation before finding significant difference among collections was 420 m. Southwest populations were very different from Intermountain populations.	1) Rehfeldt 1994
Picea pungens	Blue spruce, Colorado blue spruce	1) R (WY, UT, CO, AZ) 2) G	1) Common garden study with 10 populations showed distinct from Engelmann spruce and no evidence for introgression. 2) No geographic variation was detected in two common gardens with 163 open pollinated families from 42 populations. For height and foliage color, about twice as much variation was within stands than among stands. For bud-burst, about 8 times as much variation was within than among stands. Foliage color had a weak genetic correlation with height and bud-burst. Height and foliage had high "family" heritabilities.	1) Rehfeldt 1994 2) Bongarten, BC
Pinus albicaulis	Whitebark pine	1) G 2) R (CA)	1) Several studies of population differentiation (including Jorgensen and Hamrick 1997) show low levels of population differentiation. However, some significant geographic differences were noted, including genetic differentiation between western (Cascades and Sierra Nevada, CA) and more eastern (Rocky Mountains and Great Basin) regions. 2) Rogers et al. (1999) found little genetic differentiation among populations in different watersheds, but significant differentiation between tree-form (lower elevation) and krummholz clumps, and among various tree-form thickets and krummholz clumps.	1) Jorgensen and Hamrick 1997 2) Rogers et al. 1999

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Pinus contorta	Lodgepole pine	1) R (ID, WY, UT) 2) G 3) R (BC and Alberta Canada)	1) (var. *latifolia*) Much population differentiation has been documented in common gardens. There are steep clines in growth and freezing tolerance along gradients in elevation and frost-free days. This shows evidence for adaptation to heterogeneous environments. 2) (var. *latifolia*) Cone size, scale thickness and degree of serotiny varies among populations in relation to presence of red-crossbills, borer moths (seed predators), and pine squirrels. Evidence is consistent with selection on cone morphology by the interacting animals. Fire patterns may also influence cone serotiny. 3) (var. *latifolia*) Fst based on molecular markers very small, revealing little structure. However, in common gardens, growth traits had significantly higher structure (Qst) reflecting adaptation to superior establishment under different regional photoperiods, precipitation, and temperature.	1) Rehfeldt 1988 2) Siepielski & Benkman 3) Yang et al. 1996
Pinus edulis	pinyon pine, twoneedle pinyon	1) R (AZ) 2) R (CO) 3) G	1) There were differences in nearby populations from different soil types for level of heterozygosity and resistance to herbivores. Strong selection may be driving population differentiation on small spatial scale, despite high potential for gene dispersal via bird dispersed seeds and wind dispersed pollen. 2) Frequency of slow allele at Gly enzyme locus higher on cinder (lava) soils differed from that on adjacent sandy-loam soils. Significant association exists between allelic frequencies of Gly allozymes, heterosis in stomatal area of heterozygotes, and moist vs dry sites within 600m of each other. Earlier study showed significant differences in growth rate and fitness of Gly genotypes on cinder soil. 3) A broad-scale study of 11 populations spanning 1,650-3,100 elevation found that earlier, small-scale adaptive pattern of distribution of Gly alleles was consistent on range-wide basis. The correlation between a Gly allele and summer precipitation was very high and significant ($r = 0.92$). There was no correlation between allele frequency and elevation or soil type.	1) Mopper et al. 1991 2) Mitton et al. 1998 3) Mitton and Duran 2004
Pinus flexilis	Limber pine	R (AZ, CA, CO, MT, NV, UT, WY, Alberta)	Jorgensen et al. (2002) examined genetic diversity with allozymes over species range ($He = 0.186$, $G_{ST} = 0.101$). $Ho < He$ suggesting inbreeding. When grouped by regions, G_{ST} increased and F increased for Great Basin. Inbreeding was much lower in Northern Rockies than other areas, and He and P were significantly lower in Utah Rockies. Data suggest complex Pleistocene distribution and subsequent dispersal pattern post glaciation.	Jorgensen et al. 2002

Scientific name	Common name	Scale of genetic information available*	Genetic information (if more than one study, ordered as in "scale" column)	Reference
Pinus ponderosa 1) *P. p.* var. *ponderosa* 2) *P. p.* var. *scopulorum*	Ponderosa pine and Rocky Mountain ponderosa pine	1) R (CA) 2) R (AZ, CO, NM, UT) 3) R (MT)	These are a few of many studies: 1) Described G x E results from plantation of var. ponderosa sources in California spanning 7,000 ft. 2) Provenance trails of numerous populations were examined with respect to seed transfer guidelines for different varieties and regions showed adaptive pattern of clinal variation along elevation and precipitation gradients. 3) Quantified the gene flow potential and strong population differentiation of the two accepted varieties across and beyond the zone of contact in Montana using paternally inherited cpDNA, maternally inherited mtDNA, and nuclear allozyme data. In the transition zone, introgression based on cpDNA far exceeded that based on mtDNA. Mean Fst for populations on either side of the transition zone= 0.062, 0.652, and 1.0 based on allozymes, cpDNA, and mtDNA, respectively. Fst based on populations from one side of the zone of contact (within varieties) was much lower for nuclear marker and cpDNA, but not for mtDNA; Fst = 0.019, 0.033, and 1. *There are many regional estimates of Fst in this species, and several regional provenance tests. See seed transfer guidelines for ponderosa pine* .	1) Conkle 1973 2) Rehfeldt 1990 3) Latta & Mitton 1999
Pseudotsuga menziesii (Mirbel) Franco One of two varieties native to R2: 1) *P. m.* var. *glauca* (Beissn.) Franco	Douglas-fir, Rocky Mountain Douglas-fir	1) R (OR, 15,000 km^2 area) 2) R (ID, MT) 3) G (WA, OR, UT, AZ) 4) R (MT, WA, ID)	See FSH. 1) Common garden studies on seedlings of var. *menziesii* in OR (135 trees, 80 locations) showed geographic variables are associated with source location (lat., long., elev., distance from ocean, slope traits) and explain more of the variation in growth and its timing than variation in home soil. Performance gradients were detected within traditional "seed zones". 2) Common garden of 228 seedling populations from across an ecological gradient in ID and MT revealed adaptation to cold injury. Populations from harsh, cold sites were cold-hardy whereas populations from low or mild sites were less resistant to freezing. 3) For two populations from three different areas with different races, mitochondrial RAPD markers revealed low diversity within populations relative to nuclear RAPDs (Hs= 0.03 and 0.22, respectively), and low population structure (Gst= 0.18 and 0.05, respectively). Structure with respect to races was strong (Gst = 0.72 and 0.25, respectively), providing evidence for distinct races. 4) Freezing tolerance of 18 populations varied significantly. Analysis supports 3 provinces.	1) Campbell 1986, 1991 2) Rehfeldt 1989 3) Aagaard 1998 4) Rehfeldt 1978
Quercus macrocarpa	Bur oak	1) G (10 states in center of distribution, including SD and KS) 2) L (Ontario, Canada)	1) No significant geographic patterning in allozyme variation was detected for 21 populations sampled across 10 states (Gst = 0.076). High levels of genetic diversity were detected within populations (average He = 0.187, average P = 59%). High level of gene flow was detected from rare alleles analysis. 2) Study of single population (trees within 200 m of each other) showed significant substructure at small spatial scale (< 20 m) for 2 of 9 alleles.	1) Schnabel & Hamrick 1990a 2) Geburek & Tripp-Knowles 1994

*Scale of genetic information: G=Rangewide study; R=Regional study; L=Local or fine-scale genetic structure. Indicates coverage of studied populations.

Table 10.4. Region 2 native plant species that have variable ploidy levels (cytotypes). Comments include notes on predominant type, crossability of cytotypes, distribution of cytotypes within and among populations, associations between cytotype and habitat or morphology.

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Grasses:				
Andropogon gerardii	Big bluestem	2n = 20,40,60,70,80,84-86,90	Enneaploid (90 = 9x) was found to be larger and taller than hexaploid (60=6x). Seed production was more efficient in hexaploid but no difference in per area seed production. Might be differences among cytotypes that are maintained by natural selection. Plant predominant cytotype for area. Cytotypes cross freely and form progeny of varying chromosome numbers.	Keeler & Davis 1999; Norrmann et al. 1997
Andropogon halii	Sand Bluestem	2n = 60,70,100		Keeler & Kwankin 1989
Bouteloua gracilis	Blue grama	2n = 21, 28, 35, 40, 42, 61, 62, 77, 84	Aneuploid, assume x = 7. Study of samples from 38 locations from Canada to s.w. US (including AZ, KS, IA, WY, NE, CO, NM) grown side by side in nursery (Fults 1942); grouped into six "biotypes" that corresponded to distinct northern prairie and southwestern bunch-grass forms and four less distinct forms based on measurements of leaf, inflorescence, and flowering time; 2n= 21, 28 (tetraploid, salt flat biotype); 2n=35 (pentaploids); 2n=42 (hexaploid-- ; common type); and 2n= 61 and 77.	Fults 1942
Boutelous curtipendula	Side-oats grama	2n = 20-21, 28,35,40-46, 48,50,52-56,58-60, 62,64,70,74,76,78,80,82,84, 86-92, 94, 96,98,100-102,104		Keeler & Kwankin 1989
Boutelous hirsuta	Hairy grama	2n = 20-21, 28, 37, 40, 42,46		Keeler & Kwankin 1989

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Bromus carinatus	California brome	Harlan 1945 suggests is variable-- needs verification	Four different chromosome numbers reported in *B. carinatus complex.* Crosses made within *B. carinatus* complex n= 28, n= 21 (tetraploid x octoploid).	Harlan 1945b, Stebbins & Tobgy 1944
Buchlöe dactyloides	Buffalo grass	Four known ploidy levels (x=n=10): 2x, 4x, 5x, 6x	Ploidy level tends to increase with precipitation in this species. Both diploids and pentaploids are rare in nature-- diploid (2x) plants have been found in TX, NM, and MEX; pentaploid (5x) plants in NE, CO, NM, and TX. Cultivars 315 and 378 are 5x, which is not lilely to bode will for hybrids in natural populations.	Huff et al. 1993, Johnson et al. 1998, Budak et al. 2004
Elymus canadensis	Canada wild rye	2n = 28, 42		Keeler & Kwankin 1989
Koeleria macrantha (Ledeb.) J. A. Schultes (incl. *K. cristata, K. gracilis, K. nitida*)	Prairie junegrass, crested hairgrass	2n = 14, 28	Inaccurate citations of cytotypes cleared up in Arnow (1994). Verified counts of 2n = 14 reported from populations in mesic, high mountains of CO.; plants with 2n = 28 from driest sample areas, including w. of Rocky Mtns. in sagebrush-grassland. *Matching of cytotypes and habitats may be important to prevent outbreeding depression and maladaptation.*	Arnow 1994
Panicum virgatum	Switchgrass	2n = 18, 21,25,30,32,36, 54,70,72,90,102	Mating between tetraploids and octoploids results in a high proportion of inviable seeds; worse when the tetraploid served as the mother; cytotype and complex correlations with habitat explained most of the variation in crossing success among cytotypes and populations. Bivalent pairing after hybridizing upland and lowand cytotypes suggests homologous. However, Martinez-Reyna found postzygotic mechanism of cytotype incompatibility. (can call outbreeding depression). *Avoid mixing cytotypes until have completed studies that address fitness.*	Martinez-Reyna et al. 2001, Martínez-Reyna & Vogel 2002; Casler et al. 2004

Scientific name	**Common Name**	**Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)**	**Comment**	**Reference**
Phalaris arundinacea	Reed canarygrass	2n = 14, 27-31, 35,42	.	Keeler & Kwankin 1989
Poa alpina	Alpine bluegrass	2n = 30 to 50	Agamospermy, biotypes normaly aneuploid. Meosis in apomictic biotypes generally irregular with chromosome elimination. It is difficult to avoid mixtures of cytotypes within populations and it is not likely important to keep separate in planting projects.	Muntzing 1969
Poa secunda	Sandberg bluegrass, Canby bluegrass, big bluegrass	2n = 44,56,61-66,68,70-72,81-106	Aneuploid. Combination of apomixis, selfing, and outcrossing. Mixtures of cytotypes can occur in single population (e.g., 2n = 56,91,145, Hiesey and Nobbs 1982). Pollen stainability is variable but generally high (25-100%) suggesting generally high pollen viability. Crosses among divergent populations and cytotypes (e.g., 2n = 64 x 84), produced F1s that were 70% apomictic, but low seed fertility (40%). Another cross (2n = 62 x 84; low elev. x high elev.), produced only 5 F1 hybrids, but all were fertile in F2 and lacked apomixis. Plants cope with divergent cytotypes and crossing failure through facultative apomixis. Species have variable chromosome numbers, high polyploidy, and facultative apomixis.	Heisey & Nobs 1982; Kellogg 1985, 1987, 1990
Spartina pectinata Link	Prairie cordgrass	2n = 28,40,40+, 42,84		Keeler & Kwankin 1989
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed	2n = 18, 36, 38		Keeler & Kwankin 1989
Stipa comata	Needle-and-thread	2n = 44, 44-46		Keeler & Kwankin 1989

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Stipa viridula Trin.	Green needlegrass	2n = 82, 88		Keeler & Kwankin 1989
Herbs, other graminoids, subshrubs:				
Achillea millefolium L. 1) *A. m.* var. *alpicola* (Rydb.) Garrett (= *A. lanulosa* Nutt. ssp. *alpicola* (Rydb.) Garrett) 2) *A. m.* var. *occidentalis* DC. (= *A. lanulosa* Nutt.; *A. lanulosa* var. *typica* Keck; *Achillea rosea* Desf.)	1) Common yarrow 2) Western yarrow	2n = 18,27,36,45,54,63, 81; represents 2x-7x, 9x (includes species complex with all varieties)	Hybrids from crosses among cytotypes and taxa were often fertile. Crosses between hexaploids and tetraploids produced pentaploids that were less fertile than offspring of crosses within cytotypes (Hiesey & Nobbs 1970). *A. m* . var. *millefolium* from Europe was included in the study. Note: current taxonomy is different from that of 1940 and 1970 publications. Numerous US cytotypes and taxa are no longer considered to be other species and are now lumped into two varieties of *A. mellifolium* (USDA, NRCS 2004)].	Clausen, Keck & Hiesey 1940, Hiesey & Nobs 1970
Antennaria parvifolia	Small-leaf pussytoes	2n = 56,84,112,140; represents 4x,6x,8x,10x	Dioecious species with combination of sexual plants and apomictic plants at all ploidy levels. In growth chamber study, apomictic plants less sensitive to environment (Bierzychudek 1989). They also exceeded sexual plants in survival and flower production. In this situation, it is difficult to predict the long-term effects of hybridization between different cytotypes or ecologically differentiated plants. If the high ploidy hybrids have low fertility, their asexual lines may be evolutionary dead ends, but they may be able to persist and spread through apomixis if they happen to have broad environmental tolerance.	Bayer & Stebbins 1989, Bierzychudek 1989

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Antennaria rosea *F* our subsp: 1) *A. r.* ssp. *rosea* 2) *A. r.* ssp. *arida* 3) *A. r.* ssp. *confinis* 4) *A. r.* ssp. *pulvinata*	Rosy pussytoes	2n = 42, 56, 70 represents 3x,4x,5x	Study of geographic variation and distribution of cytotypes from 63 populations in western N. America. Both sexual and apomictic seeds produced. Most populations are tetraploid. Populations clonal with few allozyme genotypes per population. This species is thought to have formed from hybridization among as many as 8 sexual species of *Antennaria* . Polyploidy and apomixis may buffer low fertility upon hybridization, but not breakup of local adaptation. Species is thought to have formed from hybridization (see Table 10.5). Plants have not been tested for broad ecological tolerance.	Bayer 1990
Artemisia ludoviciana	White sagebrush, Louisiana sagewort	x = 8, 2n = 16, 32, 48	The *A. ludoviciana* species complex can be diploid, tetraploid, or hexaploid.	Taylor & McArthur 2004
Aster ericoides	White aster	2n = 10, 20		Keeler & Kwankin 1989
Campanula rotundifolia	Harebell, bluebell bellflower	2n = 34, 68	Different subspecies in Europe have different cytotypes. *C. r.* subsp. *rotundifolia* is 2n = 68.	Alsos et al. 2003
Carex scopulorum	Rocky Mountain sedge	2n = 36, 37, 38, 40	Polyploidy, aneuploidy, and chromosome fragmentation are common. Chromosome numbers are variable. Behaves as diploid (disomic).	Linhart & Gehring 2003
Chamerion angustifolium	Fireweed	2n = 36, (54), 72. Diploids and tetraploids, some triploids	Populations often one dominant cytotype; diploids and tetraploids have a narrow overlap zone along Rocky Mtns. In this zone (southern MT, northern WY) diploids and tetraploids are mixed and occur in mosaic pattern along an elevational gradient. *Plants from hybrid zone should only be planted back to zone. Elsewhere plant dominant cytotype.*	Husband & Schemske 1998

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Potentilla gracilis Dougl. ssp. *nuttallii* (Lehm.) Keck (=*P. g.* var. *fastigiata* (Nutt.) S. Wats.)	Northwest cinquefoil, Nuttall's cinquefoil	2n = ca. 52,54,56,57,58, 59,62,63,64,68,70,72,78,80, 84,101,103,109	Mid-altitude, subalpine, alpine, and Great Basin ecotypes.	Clausen, Keck & Heisey 1940
Solidago gigantea Ait.	Late goldenrod	2n = 18, 36, 54		Keeler & Kwankin 1989
Shrubs:				
Artemisia tridentata 1) *A. t.* ssp. *tridentata* 2) *A. t.* ssp. *vaseyana* 3) *A. t.* ssp. *wyomingensis*	1) Basin big sagebrush 2) Mountain big sagebrush 3) Wyoming big sagebrush	1, 2) 2n = 18, 36; 3) 2n = 36	In larger geographic survey of cytotypes, *A. t.* ssp. *tridentata* was mostly diploid with about 11% of populations tetraploid; *A. t. ssp. vaseyana* was about 38% tetraploid; and *A. t. wyomingensis* was 100% tetraploid. 2x plants were larger than 4x plants which are adapted to drier sites. Hybrid zones in contact areas.	McArthur & Sanderson 1999
Atriplex canescens	Fourwing saltbush	Eight ploidy levels (2x-14x, 20x)	Over 20 races named (differing in ploidy, geographic area, morphological or chemical traits). Four seed zones recommended in western US and Great Plains. Caution advised in collecting in overlap zones of tetraploids and diploids. These can hybridize and hybrids are often tetraploids that can't cross back with diploid parents.	Sanderson & McArthur 2004
Atriplex confertifolia	Shadscale	Five ploidy levels (2x to 10x)	Photosynthetic rates differ among some cytotypes: highest in 10x, lowest in 2x, and similar among 4x,6x,8x. Possibility that the variation is adaptive.	Warner & Edwards 1989

Scientific name	Common Name	Chromosome number(s) 2n = number of pairs; x = number of pairs in diploid (base number of pairs)	Comment	Reference
Chrysothamnus viscidiflorus	Low rabbitbrush, yellow rabbitbrush	x = 9, 2n = 18, 36, 54	Mostly diploids, tetraploids, and hexaploids (triploids and pentaploids occassional). In subspecies *viscidiflorus*, *lanceolatus*, and *viscidiflorus*, polyploids are adapted to lower and drier sites than diploids.	Anderson 1986, McArthur & Taylor 2004b
Trees:				
Populus tremuloides	Quaking aspen	2n = 38 = x, diploids	Triploids and tetraploids also reported, but uncommon. Ploidy not expected to be problematic.	Einspahr & Winton 1977

Table 10.5. Species from Region 2 studied for inbreeding or outbreeding effects. Note that all but *Artemisia tridentata* are herbaceous species. There is a bias toward studying herbacous species. Under Mating system column, outcrossing rate (t) is reported if known. Blank cells of table are missing data. No data found (—).

Scientific Name	**Life cycle (parity)**	**Mating System** (outcr. rate, t)**	**Evidence for inbreeding depression? (within or between population)**	**Evidence for outbreeding depression? (spatial scale of test)**	**Comment**	**Reference**
Grasses:						
1) ***Elymus glaucus*** ssp. *glaucus* 2) *E. g.* ssp. *jepsonii* 3) *E. g.* ssp. *virescens*	P	PS	—	Possibly (75 mi transect from 250- 8,400 ft elev. in CA)	24 populations from along ecological gradient grown together, crossed, and offspring tested for fertility in a common garden. 17 of 30 population crosses produced seeds; crosses among most of the ecologically divergent populations produced sterile F1s, weak, non-flowering plants, or seeds that did not germinate. Very few F1 crosses produced F2 seeds; two F2 sibships survived and were more fertile than the F1. Within population crosses not included and problems in interpretation arose due to growing conditions. *Populations are highly differentiated (Table 10.3) and plants capable of outcrossing (Table 10.1), so mixing ecologicially diverse populations could result in outbreeding depression if flowering overlaps and plants hybridize.*	Snyder 1950
Danthonia spicata	P	M	no (w)	—	Survival and reproduction of plants from seeds of open, chasmogamous flowers (CH) and closed, cliestogamous flowers (CL) were compared for three years in field plantings. There was a small, non-significant lower survival rate for CL seeds. This was not a definitive test for inbreeding depression The amount of selfing within CH flowers was not known and not all fitness components were examined.	Clay & Antonovics 1985

Scientific Name	Life cycle (parity)	Mating System** (outcr. rate, t)	Evidence for inbreeding depression? (within or between population)	Evidence for outbreeding depression? (spatial scale of test)	Comment	Reference
Herbs, graminoids, subshrubs:						
Achillea millefolium 1) *A. millefolium.* var. *alpicola* (= *A. lanulosa* ssp. *alpicola* 2) *A. m.* var. *occidentalis* (= *A. angustissim* ; *A. aspleniifolia*, *A. lanulos* ; *A. lanulosa* var. *typic* ; *A. rosea* ; *A. occidentalis*)	P		—	Within N. Amer. forms: no (range- wide within cytotypes) yes and no (range-wide among cytotypes)	1) Hybrids among widely divergent tetraploid (n= 18) and among hexaploid forms were highly fertile. Crosses among cytotypes produced pentaploids of varying fertility. Some crosses resulted in heterosis in F1 and F2 generations; some outbreeding depression; some hybrid breakdown evident in F2 generation. Some results dependent on environment of common garden. More stressful environments could aggravate outbreeding depression.	1) Hiesey & Nobs 1970
Aquilegia caerulea	P	M (I)	1) yes (w)	—	1) Study of CO population with intermediate outcrossing had strong inbreeding depression in seed production and juvenile performance. In the field, more selfed seeds aborted than outcrossed seeds and inbred offspring had lower survival and growth. Inbred offspring were less than half as successful as outbred offsrping. 2, 3) Outcrossing rates variable within and among populations. Suggests could be very strong inbreeding depression where outcrossing rate high. This high inbreeding depression suggests mixing nearby populations could be beneficial. However, correlations in floral morphology, mating system, and pollinators (Table 10.3) suggest there could be ecological outbreeding depression if mix populations with divergent floral forms (e.g. the different varieties).	1) Montalvo 1992, 1994 2) Brunet & Eckert 1998 3) Brunet & Sweet 2004

Scientific Name	**Life cycle (parity)**	**Mating System** (outcr. rate, t)**	**Evidence for inbreeding depression? (within or between population)**	**Evidence for outbreeding depression? (spatial scale of test)**	**Comment**	**Reference**
Arabis fecunda	P	M	yes (w)	—	Under greenhouse conditions, dry weight of selfed plants was lower than outcrossed plants. Seeds did not differ in number or weight.	Hamilton & Mitchell-Olds 1994
Astragalus linifolius	P	M	yes (w)	—	Rare species limited to few populations	Karron 1989
Campanula americana L. (= *Campanulastrum americanum* (L.) Small)	A	M	—	yes (> 100 km)	Crossed individuals from populations that varied in site proximity and genome size. Study populations from NC, VA, and IN. Autopolyploid. Genome size did not affect F1 hybrid performance, but proximity did. Close by crosses resulted in heterosis, far crosses in outbreeding depression.	Galloway & Etterson 2004
Chamaecrista fasciculata	A	M (t= 0.65 to 0.92) mean t = 0.80	yes (w, b)	yes (>2,000 km)	1) Often heterosis in F1; hybrid breakdown in F3 for most distant pairs of populations; F3 fitness depended on particular pair of populations; sometimes higher and sometimes lower than mean of parental populations.	1) Fenster & Sork 1988, Fenster 1991, Fenster & Galloway 2000
Chamerion angustifolium	P	M (t= 0.64 + 0.08)	yes (w)	yes (undefined distance-- in contact zone)	1) Inbreeding depression within diploid population. 2) Inbreeding depression of > 50% within tetraploid population. Outcrossing rate based on allozyme data. Some crosses resulted in outbreeding depression. 3)Triploid progeny of diploid x tetraploid crosses were less fit than within cytotype crosses. Gene flow between cytotypes is asymmetrical and limited. Fitness of triploids was only 9% of diploid fitness. *Contact zone of cytotypes is limited geographically. To avoid mixing cytotypes, track germplasm collection and deployment.*	1) Husband & Schemske 1995 2) Parker et al. 1995 3) Husband et al. 2002

Scientific Name	Life cycle (parity)	Mating System** (outcr. rate, t)	Evidence for inbreeding depression? (within or between population)	Evidence for outbreeding depression? (spatial scale of test)	Comment	Reference
Delphinium nuttallianum (=*D. nelsonii*)	P	M	yes (w)	yes (w , <100 m)	F1 outbreeding depression on small scale within populations (cumulative fitness). Suggests potential for differentiation on small spatial scale. Should look into larger scale effects.	Price & Waser 1979, Waser & Price 1994
Erythronium grandiflorum	P	OC (t=0.831 and 0.808)	yes (w)	yes (b) (<=4000 km) and > 16000 km)	1) Hybrids from crosses between subspecies (*grandifloum* and *candidum*) had lower fruit set and F1 survival in common garden than mean of crosses within varieties. (*E. g* . ssp. *candidum* is from WA, ID, and MT.) 2) In ssp. *grandiflorum* , fertilization with self pollen and pollen from within 1 m resulted in higher ovule abortion rates and fewer mature seeds than ovules fertilized with 10 m or 100 m pollen. Differential abortion increased with low nutrients. High abortion rate explains the high outcrossing rate measured on mature seeds. *If subspecies are mismatched to sites, there is a high potential for outbreeding depression.*	1) Fritz-Sheridan 1988 2) Rigney 1995, Rigney et al. 1993.
Gaillardia pulchella	A	OC	yes (w)	yes (among varieties and cytotypes)	1) Compared compatible full sib crosses with outbred crosses. Establishment of inbreds was lower than for outbreds. 2) Pairing irregularities in hybrids between divergent populations, such as between two varieties, resulted in similar to sharply lower pollen viability than non-hybrids.	1) Heywood 1993 2) Stoutamire 1955, 1977 Heywood & Levin 1984
Geranium caespitosum	P	M	yes(w)	—	Self pollen yielded more embroy abortion, fewer and smaller seeds than outcross pollen. Self pollen tube success < outcross (cryptic SI).	Hessing 1988, 1989a

Scientific Name	**Life cycle (parity)**	**Mating System** (outcr. rate, t)**	**Evidence for inbreeding depression? (within or between population)**	**Evidence for outbreeding depression? (spatial scale of test)**	**Comment**	**Reference**
Impatiens capensis	A	2) M (t for CH flw. 0.29-0.71)	1, 3) yes (w)	4) yes (local--small scale)	4) Weak evidence for a decline in fitness from crosses more than 30 m apart.	1) Mitchell-Olds & Waller 1985, 2) Waller & Knight 1989, 3) Schmitt & Gamble 1990, 4) McCall et al. 1991
Ipomopsis aggregatta	S	OC	yes (w, b)	yes (local--small scale)	1) F1 outbreeding depression, small scale within populations. Lifetime fitness was higher for intermediate (~10-20 m) crosses then 1 m and 100 m. distant populations 2) Plants from smaller populations were smaller and had higher mortality than plants from larger populations. Heterotic crosses among populations suggest there is inbreeding depession within small populations. 3) Evidence for environmental dependence of outbreeding depression.	1) Waser & Price 1989 2) Heschal & Paige 1995 3) Waser, Price, & Shaw 2000
Lobelia cardinalis	P	M	1, 2) yes (w)	2) no (1.5-170 m; > 15 km) 3) no (many km)	1, 2) Both studies found substantial inbreeding depression in seed number and mass. 2) Crossing distance within populations or among populations (regionally local scale) in terms of seed number, mass, and germination was not affected by interplant distance (no F2 or backcross data) 3) F1 generation hybrids between local and non local populations, and with introduced cultivars, showed heterosis in seedling establishment. *Results indicate some mixing of locally adapted populations may be beneficial to reduce adverse effects of inbreeding. Because of hybrid vigor in F1, backcrossing and introgression may be likely. Need F2 results to see if hybrid breakdown or continued heterosis in subsequent generations.*	1) Johnston 1992 2) Schlichting & Devlin 1992 3) Johnson 2003

Scientific Name	Life cycle (parity)	Mating System** (outcr. rate, t)	Evidence for inbreeding depression? (within or between population)	Evidence for outbreeding depression? (spatial scale of test)	Comment	Reference
Lobelia siphilitica	P	PO	1, 2) yes (w)		1) Compared selfed and outcrossed progeny and found inbreeding depression at seed maturation stage, and flower production. Overall, from seed to flowering after two years of tesing in the field, inbred progeny were only 53% as fit as outbred progeny. 2) Hermaphrodites and gynodioecious plants had cumulative inbreeding depression (seed through fist flowering) of 30% and 15%, respectively.	1) Johnston 1992 2) Mutikainen & Delph 1998
Mimulus guttatus	A/P	6) M (mean t = 0.6, ranges from t= 0.25-1.0)	1) yes (w) 3) yes (w & b) 5) yes (w)	2) yes (many km) 4) yes (differentiated populations in species complex)	1) California population with 47% outcrossing had selfed progeny 19% as fit as outbred progeny. 2) Heterosis for seed set in F1s but hybrid breakdown in F2 where mean seed set was reduced to below the mean of the original parents. Some combinations of distant populations produced good seed set while others resulted in very low seed set. 3) Fitness increased with distance of cross. 4) In crosses with *M. nasutus* , hybrid breakdown in fertility traits observed in F2. 5) Deleterious recessive alleles were responsible for most of the inbreeding depression in mixed mating *M. guttatus* and the closely related, but selfing, *M. micranthus* .	1) Willis 1993, Dole & Ritland 1993 2) Vickery 1958 3) Ritland & Ganders 1987 4) Fishman et al. 2002 5) Dudash & Carr 1998 6) Carr & Eubanks 2002 This is just a sample of related studies.
Trillium grandiflorum	P	OC (t= 0.76 to 1.0)	yes, w	no (to 1500 m)	Spatial autocorrelation showed isolation by distance; Fst = 0.044 (local scale < 1650 m). Often single protandrous flower/plant so high OC rate.	Irwin 2001 (Lubbers & Lechowicz 1989 for life-history)

Scientific Name	Life cycle (parity)	Mating System** (outcr. rate, t)	Evidence for inbreeding depression? (within or between population)	Evidence for outbreeding depression? (spatial scale of test)	Comment	Reference
Shrubs:						
Artemisia tridentata 1) *A. t.* ssp. *tridentata* 2) *A. t.* ssp. *vaseyana*	P	OC	—	yes (adjacent sites; few to 100s of m)	Plants tested in hybrid zone and parental environments; F1 most fit in ecotone between the two subspecies studied; parents most fit at contrasting home sites. *Not advisable to plant hybrids outside hybrid zone or to mix taxonomic varieties outside a hybrid zone.*	Wang et al. 1997, Graham et al. 1999
Trees:						
Pinus contorta var. *murrayana*	P	M but effectively OC	yes (w)	—	Nursery test of self and outcross pollinations and progeny in nursery. Provides evidence for purging of deleterious alleles. Inbreeding depression in early life-cycle traits (embryos and seedlings). Result is low self-fertility. High inbreeding depression makes seeds look highly outcrossed.	Sorenson 2001
Pinus ponderosa 1) *P. p.* var. *ponderosa* 2) *P. p.* var. *scopularum*	P	OC (2)	1) yes (w)	—	1) Total inbreeding depression from the time of fertilization through to maturity in a common garden after 26 years of growth was very high. Total fitness of selfed ovules/trees was only 6% of outcrossed ovules/trees. 2) Lower outcrossing rates in low density stands compared to high density stands (t= 0.96 vs 0.85, respectively). Seed and seedling stages were sampled. Outcrossing rate was higher in seedling stage, suggesting loss of homozygous individuals. This is consistent with study 1, above.	1) Sorensen 1999 2) Farris & Mitton 1984

Scientific Name	Life cycle (parity)	Mating System** (outcr. rate, t)	Evidence for inbreeding depression? (within or between population)	Evidence for outbreeding depression? (spatial scale of test)	Comment	Reference
Pseudotsuga menziesii	P	OC (1,2,3,) based on multiple loci: t= 0.93-1.0, mature seeds	3) yes (w)	—	3) At pollination and fertilization stage, there is intermediate selfing. However, very high inbreeding depression results in failure of most selfed embryos. In a long-term common garden study of selfed and outcrossed progeny of *P. m* . var. *menziesii* , very few selfs reached mature seed stage and few to none of those reached reproductive maturity after 26 years in a common garden. Total fitness of selfed ovules/trees crosses was only 2% of outcrossed ovules/trees.	1) Neale & Adams 1985, 2) Ritland & El-Kassaby, 3) Sorensen 1999

*Sexual system/mode: SC= Self-compatible, SI= Self-incompatible; P= perfect; D= dioecious; M= monoecious; G= gynodioecous; H= heterostylous;

**Mating system: OC=Outcrossing, M=Mixed Mating, S=Selfing. If known, indicate if mixed mating system is PO=Primarily outcrossing; I=Intermediate; PS=Primarily Selfing)

***Inbreeding depression found: w= within population; b= between population heterosis (give scale)

****Outbreeding depression found: w= within population (small scale); b= between population (broad scale)

Table 10. 6. Ecological genetic details for *Populus tremuloides,* an example of a wind-pollinated tree species with wind dispersed seeds.

Species	*Populus tremuloides* Michx.; Family Salicaceae, Order Salicales, Subclass Dillenidae, Class Magnoliopsida (dicot)
Synonyms (PLANTS database and FEIS*)	(PLANTS): *Populus cercidiphylla* Britt. *P. tremuloides* Michx. var. *aurea* (Tidestrom) Daniels *P. tremuloides* Michx. var. *cercidiphylla* (Britt.) Sudworth *P. tremuloides* Michx. var. *intermedia* Victorin *P. tremuloides* Michx. var. *magnifica* Victorin *P. tremuloides* Michx. var. *rhomboidea* Victorin *P. tremula* L. ssp. *tremuloides* (Michx.) A.& D. Löve *P. tremuloides* Michx. var. *vancouveriana* (Trel.) Sarg. FEIS database lists several more: *P. tremuloides* var. *pendula* Jaeger & Bessner, *P. tremuloides* var. *reniformis* Tidestr.; *Populus aurea* Tidestrom
Common name	quaking aspen, trembling aspen, aspen
Subspecific taxa	None currently recognized
General: Life history, life form	Tree; deciduous, long-lived clones
Ploidy	Diploid. 2N = 38 (Smith 1943 *in* Munz and Keck 1968). Einspahr and Winton (1977) report in a review naturally occurring monoploids, triploids, and tetraploids. [note: triploid and tetraploid individuals have been induced with colchicine.]
Geographic range	Widespread. Most widespread tree species in North America. Occurs in most of Canada and into Mexico (FEIS). In the US, it occurs in all states but Hawaii and the far southeastern states. Distribution is mostly continuous in the northeast, becoming more patchy in the drier western states as it tracks suitable moist habitat.
Elevation range	Sea level to timberline depending on latitude, longitude (geographic location and climate). Occurs at sea level in northern and coastal part of distribution; occurs at mid to high elevation in more southerly latitudes (occurs above 2,000 m in California and Mexico (Munz and Keck 1968; FEIS); from about 1,800 to 3,500 m in CO (Harrington 1964); and at it northern limit up to 910 m (FEIS) .
Geographic variation (morphological/physiological traits)	Plants from different elevations differ in leaf chemistry which affects patterns of herbivorous insect performance (Osier and Lindroth 2001). Regional floras mention differences in form; for example, western plants have been called var. *auria* Daniels (Harrington 1964, Munz and Keck 1969). In a common environment, 29 clones from five Alberta populations differed significantly for a few traits (Thomas et al.1997), and most variation was among clones. A Qst of 0.14 (for bud flush) was much higher than Gst of 0.068 (for allozymes), suggesting natural selection may influence variation in bud flush (Howe et al. 2003) [see Chapter 6: if significant Qst > Gst, this suggests break up of local adaptation is more likely than coadaptation.]. Hyun (1987) studied allozymes of 222 clones from eight British Columbia populations, while Thomas et al. (1998) studied quantitative traits in only 29 clones from five Alberta populations. Other *Populus,* and likely this one too, vary geographically in timing of bud flush and photoperiodic response (Pauley and Perry 1954) and have clines in traits associated with adaptation to cold (Howe et al. 2003).
Genetic variation and population structure	Diversity statistics vary considerably among studies using different markers, regions, and life-cycle stages. In allozyme studies of adults, % P ranged from 58-90% and Hexp from 0.23-0.33 (Jelinski and Cheliak 1992, Mitton and Grant 1996). H_e ranged from 0.24- 0.72 in a microsatillite study of interdigitating clones (Wyman et al. 2003) and from 0.18- 0.24 in a study of seedling populations (Stevens et al. 1999). Differences may be due to sampling methods, but western sites with more clonal propagation than seedling recruitment tend to have excess heterozygotes; eastern, humid sites with frequent seedling recruitment tend to have a deficit of heterozygotes. Somatic mutation and higher success of heterozygous clones can increase H_e of clones over time. Within geographic regions, low population structure (Gst often ranged 0.028- 0.032) was likely due to high gene flow; values would likely increase with inclusion of multiple geographic regions. Variation within populations generally exceeded among population variation (Stevens et al. 1999), but diversity in seedling populations of Yellowstone was higher than for pre-fire mature clones sampled nearby (Turner et al. 2003).

Species	*Populus tremuloides* Michx.; Family Salicaceae, Order Salicales, Subclass Dillenidae, Class Magnoliopsida (dicot)
Correlates of genetic variation	Mitton and Grant (1980) studied variation in growth rate within and among clones over elevation gradient in CO Front Range using allozyme markers. 54% of variance within ramets among years; 14% among ramets of a clone due to microsite heterogeneity; 33% of variance among clones of same sex. No variance explained by difference in sex. Rough estimate of broad sense heritability in growth rate (ignoring non-random growing positions) had upper bound of 32.6%. Also found that mean growth rate increased with mean clone heterozygosity.
Habitat affinity	Many sites in areas with moist climate or along streams in arid climate. Often in mid to upper riparian areas. Often dominant species in species matrix that changes with location.
Growth pattern	Winter dormant, deciduous.
Breeding system/Mating system	Dioecious (whole clones either male or female), rarely with some perfect flowers. 100% outcrossing except when some perfect flowers present. Unconfirmed reports of sex chromosomes (Mitton and Grant 1980). Flower and seed production variable and subject of past debate. Sex ratio of clones is usually 1:1. Tends to be less successful seed production where relative humidity low.
Pollen dispersal	Wind pollinated. In a pollen trap study, Wright (1953) found two other wind-pollinated *Populus* species dispersed pollen 1,000 or more feet. These flowers are very similar and pollen likely travels similar distances.
Hybridization potential	Plants hybridizes with native bigtooth aspen (*P. grandidentata*) and naturalized white poplar (*P. alba*). Hybrid quaking aspen-bigtooth aspen swarms occur in several states, including WY and NE (FEIS). Heterosis occurred in some hybrids with European species (*P. tremula, P. adenopoda, P. alba,* and *P. davidiana*) in a plantation setting, but not if involving bigtooth aspen (Zsuffa 1975). Some hybrids were less resistant to diseases; severe dieback caused by the fungus *Plagiostoma populi* occurred in some white poplar-quaking aspen hybrids. The genetic basis of hybrid fitness was complex. Wu (2000) found 44% of variance in fitness of mixed generation hybrid populations with *P. tremula* was due to gene interactions (epistasis), whereas first generation hybrid progeny showed only a 10% contribution of epistasis. The form of epistatic interactions is not predictable, but will determine if fitness increases or decreases. Postpollination incompatibility barriers deter success of intersection crosses (for example with black cottonwood) and some intrasection crosses (Willing and Pryor 1976, Guries and Stettler 1976).
Vegetative propagation	Forms extensive clones through suckering. In one study, clone size ranged from few to 47,000 rametes with the largest clone covering 43 hectares (Kemperman and Barnes 1976). Stems of adjacent clones often interdigitate, especially when they resprout after fire. Genetic diversity among clones in an area is very high. Clones can be very long-lived, but verification of age is elusive (Mitton and Grant 1996). Extensive literature on clone identification, age, and size (e.g., Jelinski and Cheliak 1992; reviewed in Mitton and Grant 1996, FEIS).
Primary seed dispersal	Wind dispersed long distances, possibly kilometers, but longevity short (Fowells 1965). Tiny seeds with buoyant hairs (Mitton and Grant 1980, 1996).
Interactions with (bacteria/ herbivores/ pollinators/ fungi) vary	Variation in phytochemical composition exists among individuals, and is stronly influenced by environment (Lindroth et al. 2002). These differences influence herbivore performance (Osier and Lindroth 2001).
Seed dormancy	None. Seeds short-lived, no seed bank. Viabilty is high upon release, but drops significantly after 3-6 weeks (Fowells 1965). Seeds must find safe, moist sites quickly or die.
Taxonomic Relationships	Subsection *Trepidae* of the genus *Populus* . Quaking aspen, bigtooth aspen (*P. grandidentata*), European aspen (*P. tremula*), and three aspens occurring in Asia have been classed together as a single superspecies (Peterson and Peterson 1992).
Translocation effects/risks:	Einspahr and Winton's (1977) review of quaking aspen genetics reported that limited provenance studies concluded that western high-altitude sources were unsuited for use in Massachusetts and were probably unsuited for use in the Lake States Region. Also said marked differences have been reported in many morphological traits, in the flushing of clones, and in growth rate. Strong positive correlation exits between early flushing and frost injury. All the comparisons mentioned were within regions.

Species	*Populus tremuloides* Michx.; Family Salicaceae, Order Salicales, Subclass Dillenidae, Class Magnoliopsida (dicot)
Local adaptation	Provenance study results: In a review, Fowells (1965) reports evidence of ecotypic variation in response to photoperiod. Seedlings from northern part of range (Saskatchewan) have greater root weight and seedlings stop growing at a longer day-length than seedlings from south (Wisconsin). He suggests that greater root system is adaptation to cold. In a 26 year study in Sweden, Ilstedt and Gullberg (1993) found both parents and hybrids to be susceptible to *Hypoxlon* cancer and stem deformities and recommended against introductions.
Inbreeding and outbreeding	None found.
Regeneration after fire/other disturbance	Readily resprouts from root systems after fire, cutting, or other disturbance (Fowells 1965, Kilpatrick et al. 2003). Occasionally sprouts from stumps or root collar. Seedlings emerge from freshly dispersed seeds on moist to wet bare mineral soil after fire, disturbance (Mitton and Grant 1996; FEIS).
Use in revegetation	Yes. Seeds and cuttings. Seeds short lived and need ample moisture for successful germination and establishment.
Use in horticulture or agriculture	Yes. Ornamental tree. Important wood products.
Wildlife value (not really needed)	High: e.g., browse for deer, elk, moose; seeds for birds and rodents; bark for rodents, porcupine. Important breeding habitat for birds and mammals. Utilized by many wildlife species. (FEIS)
Plant Material Releases by NRCS and Cooperators	None listed, but is in horticultural trade. Hybrids have been produced in tree improvement programs.
***FEIS**	Howard, Janet L. 1996. Populus tremuloides. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ .

Table 10.7. Ecological genetic details for *Linum lewisii* , an insect-pollinated perennial herb with gravity/animal dispersed seeds.

Species	*Linum lewisii* Pursh.: Section *Linum* , Family Linaceae, Order Linales, Subclass Rosidae, Class Magnoliopsida (dicot)
Synonyms	*L. perenne* ssp. *lewisii* (Pursh) Hult.
Common names	Lewis' flax, prairie flax, blue flax, Lewis blue flax
Subspecific taxa	*L. lewisii* var. *lewisii* Pursh; *L. lewisii* var. *alpicola* Jepson; L. *lewisii* var. *lepagei* (Boivin) Rogers
General: Life history, life form	Perennial herb, short lived
FEIS	N/A
Ploidy	2n = 18 (Ockendon 1968).
Geographic range	Widespread from AK to Mex. In US, mostly in Great Lakes region and from Mississippi River West. (Okendon 1968, Munz and Keck 1968, USDA NRCS 2004).
Elevation range	From low to high elevation. Meyer and Kitchen (1995), Kichen (1994) used accessions from 320 feet to 3,160 feet from UT, ID, NV, and WA. In California, occurs from 4000-11,000 ft. (Munz and Keck 1968). In CO from 4500-more than 10000 ft. (Harrington1964; to 3,475 m near RMBL, Kearns and Inouye 1994)
Geographic variation: morphological	Seed germination patterns vary by elevation of source population (Meyer and Kitchen 1995, Kitchen 1994). Ockendon (1968) mentions possible geographic variation in morphological traits in species of *Linum* in Europe, including *L. perenne.*
Geographic variation: genetic markers	No studies found.
Genetic variation and population structure	Significant broad-sense heritability in seed dormancy, rust resistance, and survival in common gardens (Meyer and Kitchen 1994 and rust resistance (1995)).
Habitat affinity	Occurs in range of habitats from shrub steppe to mountain meadows.
Breeding system/ Mating system	Perfect flowers, homostylous, self compatible (Ockendon 1968), and likely mixed mating. Requires insect pollinators for seed production (Kearns and Inouye 1994). In contrast, closely related heterostylous species, *L. perenne* , is heterostylous obligate-outcrosser (has SI) (Ockendon 1968).
Major pollinators	Bees and flies. Flies often more frequent and therefore more effective, especially at higher elevations (Kearns and Inouye 1994). Twenty-five species of flies and 19 species of bees recorded, including bumblebees, but small bees most frequent.
Hybridization potential	No fertile seeds produced when crossed with European *L. perenne* L. or cultivar 'Appar' from *L. perenne* (Pendleton et al. 1993 abstract). The intra-morph self-incompatibility mechanism present in the heterostylous species (populations with genetic variation in flower morphology such that some plants have flowers with long stamens and short styles and others have short stamens and long styles) such as *L. perenne* prohibit interspecific crosses with homostylous species (such as *L. lewisii* in which flowers are monomorphic with respect to style and stamen lengths) (Ghosh and Shivanna 1984). Munz and Keck (1968) cite Baker (1965) for report of strong crossing barriers between Old World *Linum perenne* L. and New World *L. lewisii* (Huntiana 2:141-161). Ockendon (1968 identified crossing barriers through extensive crossing studies, but *L. lewisii* was not included in the crosses.
Vegetative propagation	None
Primary seed dispersal	Gravity; birds use and may disperse

Species	*Linum lewisii* Pursh.: Section *Linum* , Family Linaceae, Order Linales, Subclass Rosidae, Class Magnoliopsida (dicot)
Interactions (fungi/ bacteria/herbivores/ pollinators) known to vary	Differences in susceptibility to rust fund among accessions in common garden (Kitchen 1995). Seeds from drier sites produced plants more susceptible to rust infection and shorter lived than plants from more mesic sites. The three populations examined in greenhouse study were found to be highly dependent on associations with arbuscular mycorrhizal fungi (AM fungi that form symbiotic association with roots-- fungi receive carbohydrate from plant and plant receives some nutrients and sometimes higher water gathering potential), and significantly more so when grown in sand and sand + peat than in peat. Inoculation with crust-forming algae increased survival and root:shoot ratios. There were differences among populations in growth response to AM fungi. Populations from different locations in the Rocky Mountains experience much variation in available pollinating bees and flies (Kearns and Inouye 1994). It is not known if there are genetic differences among populations in attractiveness to different pollinators.
Seed dormancy	Ecologically relevant variation in seed dormancy and timing of germination was revealed in common garden studies (Meyer and Kitchen 1995). Seed sources varied in dormancy and response to pre-chill, as did individuals within a population. High elevation populations emerge in spring and have little carryover of seed. Low elevation populations with less predicable precipitation were more dormant. Garden-grown seeds were less dormant than wild-collected seed. In storage, seeds loose dormancy within a year of collection (Meyer and Monsen 1993).
Taxonomic Relationships	Chloroplast DNA analysis of 8 species of *Linum* placed *L. lewisii* in same cluster with *L. perenne, L. boreale,* and *L. alpinum* , substantiating previous morphological work. There was significant divergence between *L. lewisii* and all other species (Coates and Cullis1987).
Translocation effects/risks:	There is a risk of inappropriate seed germination environment when moving populations to different elevations and habitats.
Local adaptation	Timing of germination, degree of seed dormancy, and temperature effects on dormancy vary with seed source and habitat (Meyer and Kitchen 1994). Low elevation sites appeared to have a bet-hedging strategy with seed bank carryover among years.
Inbreeding and outbreeding research	No detailed studies. On average, hand self-pollinations produced one fewer seed per capsule than outcrossed pollinations (Kearns and Inouye 1994).
Regeneration after fire/other disturbance	No vegetative spread. Perennial from tough, fibrous woody base. Not likely to survive fire.
Use in revegetation	Common in restoration mixtures, roadside seeding, erosion control
Use in horticulture or agriculture	Ornamental use in xerophytic gardens, roadside plantings
Wildlife value	Moderate (USDA fact sheet available from USDA NRCS 2004).
Plant Material Releases by NRCS and Cooperators	Maple Grove' Germplasm (released by Forest Service and Aberdeen PMC in 2003). Source was Maple Grove, UT area. Selected for use from 1,000 to 6,000 feet. Not tolerant of poor drainage. 'Appar' , which has no seed dormancy, was incorrectly identified as *L. lewisii* when first released in 1980, but it was later identified as the heterostylous, European species, *L. perenne* L. 'Appar' was mistakenly used as native Lewis flax for about 10 years. Appar is used in mixtures with other species, for highway seeding, gardens, diversity, and beautification.

Table 10.8. Ecological genetic details for *Bouteloua gracilis* , a wind-pollinated bunch grass.

Species	*Bouteloua gracilis* (Wild. Ex Kunth) Lag. ex Griffiths, Familiy Poaceae, Order Cyperales, Subclass Commelinidae, Class Liliopsida (monocots)
Synonyms	*Chondrosum gracile* Willd. ex Kunth
Common name	blue grama
Subspecific taxa	None listed
General: Life history, life form	Densly tufted, warm season perennial grass, often with short rhizomes. Variable in form from bunch grass to tillering. Geophyte.
Ploidy	Variable ploidy. Tetraploid according to Fu et al.(2004). Munz and Keck (1968) report variable ploidy levels (2n = 20, 28, 35, 40, 42, 61, 62, 77, 84 (cite Fults 1942, Snyder and Harlan 1953)) which is suggestive of diploid, triploid, tetraploid to octoploid series. (See common garden below for Fults who did DETAILED cytological work.)
Geographic range	Widespread. British Columbia east to Manitoba, and south to California, Texas, and into central Mexico. Most common in the Rocky Mountains, Great Plans, and Midwest States to Mexico. Populations in Idaho and Missouri are considered sensitive (Idaho Fish and Game Department. 2002. Idaho's rare vascular plants, [Online]. Available: http://www2.state.id.us/fishgame/info/cdc/plants/vasc_plants&status_a-d.htm [2002, February 15]; Missouri Department of Transportation. 2001. Endangered species checklist (flowering plants), [Online]. Available: http://www.conservation.state.mo.us/nathis/endangered/checklst [2002, February 22].). Introduced to Michigan.
Elevation range	Broad range. Elevation range varies considerably with geographic area. For example, blue grama occurs from about 200 - 2,900 m in Utah; from 1000- 3,200 m in Colorado, and 950-2,600 m in Wyoming (FEIS).
Geographic variation: morphological	Extensive. Occurs in many different habitats (moisture patterns, exposure, soil traits, temperature, elevation, latitude) and plant associations (FEIS).
Common garden	Evidence for genetic differences. Fults (1942) examined 55 plants from 38 locations from Canada to southwestern US (including AZ, KS, IA, WY, NE, CO, NM). Grew side by side in nursery. Easily classified into six "biotypes" that corrsponded to distinct northern prairie and southwestern bunch-grass forms and four less distinct forms based on means and standard errors of leaf, inflorescence, and flowering time measurements. 2n= 21, 28 (tetraploid, salt flat biotype). 2n=35 (pentaploids), 2n=42 (hexaploid-- the common type), and 2n= 61 and 77 . Found significant differences in lengths of chromosomes from different seed sources. Riegel, A. (1940 in Malovich (2002) did two year common garden study using nine source populations from 9 states. Data table indicates there are differences among populations for traits such as tillering and anthesis. [need thesis by Miller, R. E. - common garden study in Colorado]
Geographic variation: genetic markers	RAPD markers were used to asses genetic variation in 11 natural source populations in Great Plains of Western Canada. There were no associations between genetic distance and geographic distance (Phan et al. 2003). Fu et al. (2004) compared genetic diversity among four seed sources, including: pre-varietal germplasm of multisite composit "BMSC", the exotype "Bad River", a Minnesota ecotype, and a wildland collection from Manitoba, Canada. See "Plant Materials Releases" below.
Genetic variation and population structure	For 11 natural populations separated by > 30 km, band frequency for each population averaged 0.42. Ninety-seven percent of total RAPD variation was found within natural populations, with 3 percent among populations (Phan, Fu, and Smith 2003). No species level study on population structure found. Suggests high gene flow potential.
Habitat affinity	Occurs in many different habitats and plant associations throughout its native range: aspen parklands in Canada, understory of riparian cottonwood forests in the Central Plains, sagebrush steppe, big sagebrush, in the Great Basin, in salt-desert shrub communities in the southwest, in evergreen oak woodlands of the southwest, ponderosa pine forest in the Rocky Mountains, pinyon-juniper in the southwestern USA, and in many grassland associations of the Great Plains and southwestern regions, including shrotgrass prairie, mixed prairies, and semi-desert grasslands. Often a dominant or co-dominant species.
Mating system	Outcrossing. Fankel & Galun (1977) report outbreeding with some forms apomictic (agamospermous).

Table 10.8. Ecological genetic details for *Bouteloua gracilis* , a wind-pollinated bunch grass.

Major pollinators	Wind pollinated
Hybridization potential	Not found
Vegetative propagation	Plants can be propagated by tillers (McGinnies et al. 1988). Tillering ability may be variable (FEIS).
Seed dispersal	Wind, insects, hitch-hiking on mammal fur, and ingestion by large animals (FEIS)
Growth pattern	Warm season grass with vegetative growth primarily in spring through early summer, depending on location. Flowering varies geographically but is primarily in July- August with shoots scenescing in October-November. (Any genetic differences growth patterns may be important to plant survival/reproduction and important species interactions.)
Interactions (fungi/herbivores/ pollinators) known to vary	Recorded as only larval food plant for FT Pawnee mountain skipper (*Hesperia leonardus montana*) in field study in CO (Wooley et al. 1991). [note: Need to know if there is a tight correspondence between timing of plant growth and larval growth that would be affected by use of plant populations that differ in timing of growth or other factors that affect larval development.]
Seed dormancy	Transient seeds, few seeds stored in soil (Coffin and Lauenroth 1989. AJB 76:53-58). Dry storage promotes germination to 95% (in Baskin and Baskin 1998). This means good seed bank after fire is unlikely.
Translocation effects/risks	(Need to see results of common garden studies and effects of different phenology on interacting species.)
Local adaptation	Still need to see Miller, R.V. 1967 (masters thesis on ecotypic variation in CO)
Inbreeding and outbreeding	Not found
Regeneration after fire/other disturbance	Postfire recovery variable and season dependent, but tends to improve after fire. Low density tufts survive fire, especially in dormant season, and following good rainfall years. In studies in Kansas, Montana, South Dakota, and North Dakota, cover increased after fire, but in a Nebraska study cover decreased. Regeneration also occurs by on and off-site seed. Cover also tends to increase after overstory removal in pinyon-juniper forest.
Use in restoration	Extensive use in restoration and reclamation, and erosion control in arid and semi-arid regions.
Use in horticulture or agriculture	Widely used for livestock pasture and sometimes for hay. Used as ornamental (Grass Manual).
Wildlife value	Important forage for deer, elk, pronghorn, bighorn sheep, bison. Seeds eaten be variety of birds and small mammals.(FEIS). Larval food plant for TES moth species, Pawnee montane Skipper (*Hesperaia leonardus montana*) (Wooley et al. 1991).
Plant Material Releases NRCS and Cooperators Cult=cultivar, N=native to USA, Sel=selected	Alma' (cult., composite, '1992 ARS); Bad River Ecotype (sel., Haakon Co., SD, '1996); 'Hachita' (cult., Hachita Mountain, NM, '1980); 'Lovington' (cult., Lea Co., NM, '1963); Minnesota ecotype (sel.,Lake Bronson MN, 1995). Efforts since 1992 to produce seed adapted to western Canada-- BMSC is a pre-cultivar developed in 2000 from a selection of 99 clones from 495 plants collected from 11 sites across Manitoba, Canada (balanced multisite composite) (Fu et al. 2004). Genetic diversity of BMSC Manitoba, Bad River ecotype (selected class), Minnesota ecotype (commercial increase), and a third generation harvest from BMSC were compared for AFLP variation to detect genetic shifts. For BMSC, there was a non-significant decrease in genetic variation after 2 cycles of seed increase. BMSC had the highest genetic diversity among the germplasms sampled. BMSC was also shown by canonical discriminant analysis of RAPD data to have undergone slight genetic shifts relative to the 11 source populations from which it was derived (Phan et al. 2003).
Seed Transfer Guidelines	Draft Guidelines, Mary F. Mahalovich, Dec. 4, 2002. DRAFT document.
FEIS	Anderson, Michelle D. 2003. *Bouteloua gracilis* . In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2004, April 22]

Further resources

As stated above, not all species of interest to Region 2 are covered in the tables presented here, and very few non-woody species have seed transfer guidelines. As explained in Chapter 6, seed zones with firm boundaries can be updated and converted to continuous seed transfer rules on a species by species basis. The type of information presented in the tables could be useful in development of future interim guidelines (or directives if a handbook is prepared for non-woody plants). For woody species, the information could be used to aid future interim directives or revision of the Seed Handbook. An ecological genetics database that parallels the Forest Service "Fire Effects Information System" internet database (FEIS 2004) would be helpful to Readers of this Guide. The FEIS database provides extensive reviews of the general ecology of about 900 plant species. Although the emphasis is on how fire affects each species, many of the reviews contain some basic information important to selecting sources of plants, including information on life form, elevations, habitat affinities, regeneration after fire, geographic distribution, taxonomic synonyms, and establishment. This database was helpful in providing some of the information for Tables 10.1-10.2, especially.

Parallel reviews of the ecological genetics of plants and attributes that affect population differentiation would facilitate informed genetic decisions for many more species before official seed transfer guidelines become available. A large body of information on the ecology and genetics of plants sits waiting to be gleaned from academic, applied, and government volumes so it can be put to use.

In the meantime, there are valuable search tools and databases available to users of this Guide. The tools can help find information to guide decisions for those species not contained in the tables and to augment the tabulated information as new information becomes available. The search for such information is becoming easier and more accessible to individuals in remote locations. Every day, more literature is available on-line and can be found with the help of electronic search engines. Many of the citations pointed to in an electronic search can be found online. For example, all volumes of eleven botanical journals (including the *American Journal of Botany*, *Systematic Botany*) and 25 ecological/evolution journals (including *Ecology*, *Ecological Monographs*, *Evolution*, *American Naturalist*) are available on line from JSTOR® (2004), an internet archive for scholarly journals. JSTOR journals can be searched using plant names and title words. Information about what institutions and agencies have subscriptions (education institutions and agencies from all states in Region 2 are listed) is also provided on the JSTOR site. Some journals, such as *The Journal of Range Management*, have independently made most back issues available. In addition, many professional societies and publishers of journals, including most genetic journals, have made many issues available online with a subscription.

USDA employees have access to a number of powerful library search programs, including BIOSIS, AGRICOLA, and CAB ABSTRACTS through "DigiTop," on the web site of the National Agricultural Library(USDA NAL 2003). Electronic viewing and downloads are available through the site for recent articles in many journals, including Crop Science, Restoration Ecology, Ecological Applications, Canadian Journal of Botany, and Science.

The following online resources are useful for finding information about plant taxonomy, evolution, and ecology.

Online resources

Colorado Natural Heritage Program. 2004. http://www.cnhp.colostate.edu/.

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Chapter 11

Demonstration of Using the Guidelines to Choose Appropriate Genetic Materials

Chapters 1 through 8 have been developed with the goals of explaining the significance of genetic diversity and reasons for maintaining it in native plant species, describing genetic diversity and its influences, explaining various ways to measure and represent genetic diversity, and examining some consequences of introducing plants onto sites from inappropriate genetic sources. To the extent those messages have been presented clearly, this heightened level of awareness about genetic diversity is the best guide for making decisions. The guidelines in Chapter 9 provide prompts to consider the various kinds of information that have been explained earlier as relevant to genetic source decisions.

For demonstration purposes, three species have been selected with diverse characteristics and varying amounts of available genetic information. For each, provided below is an example of how one might work with the decision guidelines in Chapter 9, consulting the tables in Chapter 10. The information used is real, but the situation (site context and objectives) is hypothetical. Ten points are provided for each species—each corresponding to a numbered step in decision guidelines.

The comments at the end of each example briefly summarize the salient information and suggest how this can be applied to the decision. However, there will often be additional information about the site conditions, site context, or additional information about the species (as the tables in Chapter 10 may not reflect the most recently available information) that should also be taken into consideration.

Example 1: *Carex scopulorum* Holm. (Rocky Mountain sedge)

Figure 11.1. Rocky Mountain sedge (*Carex scopulorum*). USDA-NRCS PLANTS Database / Hurd, E.G., N.L. Shaw, J. Mastrogiuseppe, L.C. Smithman, & S. Goodrich. 1998. *Field guide to Intermountain sedges*. Gen. Tech. Rep. RMS-GTR-10. USDA FS RMRS, Ogden, UT.

1. In this hypothetical case, the main goal of the revegetation project is to restore a healthy population of this sedge after years of trampling, soil compaction, and habitat rutting caused by extensive off-road ATV use of the area. There are no other major project objectives. So we skip to number 3, based on these objectives.
2. Step 2 is skipped.
3. Although this species has some capacity for vegetative reproduction (particularly after a fire), the site disturbance has been such that we have no confidence in the potential for natural regeneration to allow this species to recover locally. It is decided that some plant introduction for this species is necessary.
4. The species is not listed as protected on the federal list or on any state list in Region 2, so no additional laws or rules apply to guide restoration.
5. There are no seed transfer rules available for this species. It is noted (from Table 10.1, Chapter 10) that this perennial herb has three recognized varieties. It is self-compatible, and disperses pollen by insect vectoring and by wind. So it would be important to identify the appropriate (local) subspecies. The insect vectoring of pollen might suggest that there is more local spatial genetic structure than if pollen was only wind-dispersed.
6. This species is able to grow clonally via rhizomes (Table 10.2, Chapter 10). The species is monoecious (Table 10.1). One study showed that clones were fairly small. But it is uncertain if the species consistently has this pattern of small clone sizes in other areas (beyond the study area) within Region 2. The same study suggests there is considerable sexual reproduction in the species also.
7. One study in Colorado shows that even though this sedge can reproduce asexually through rhizomes, the clones in this area were fairly small and there was considerable genetic diversity (Table 10.3, Chapter 10). Furthermore, there is some evidence of adaptation relative to different moisture levels (from very wet bogs to moist meadows), and

neighboring clones were not necessarily more closely related to each other than clones farther away. The three varieties are distinguished to some extent by the elevation at which they grow, so matching elevation is important in selecting the appropriate variety (if they are otherwise hard to distinguish).

8. This sedge is known to have various ploidy levels (Table 10.4, Chapter 10). One study of one variety (*C.* var. *s. scopulorum*) showed that it behaved like a diploid (disomic inheritance). The ploidy level or levels of the resident (on or near project site) plants is not known. Because of disomic inheritance, the different ploidy levels are of less concern here. Probably choosing the appropriate variety, elevation, and fairly local geographic source will also be adequate for selecting correct ploidy level.
9. The species is self-compatible. No specific information is available on its mating system (Table 10.1, Chapter 10) but it likely has a high level of outcrossing. There is no information on inbreeding or outbreeding depression.
10. The soil has been compacted by frequent ATV use. Moisture levels on site are probably sufficient to provide suitable habitat to planted plugs as long as the site is protected from ATV use in the future.

Comments: The unknown distribution of different cytotypes, and the evidence of local adaptation for site moisture levels, suggests that revegetation materials should be collected from similar site types (particularly relative to site moisture: standing water, meadow, bog, or drier area) and for the same variety of the species (which are associated with different elevations). Although there is some reproduction by rhizomes, there is no evidence of very large clones. Even though there is evidence of considerable sexual activity, there is no evidence that plants that are closer to one another are more closely related than those further apart. So this can be collected as though it was a sexually reproducing species (although keeping aware of the possibility of several adjacent plants being the same clone, and thus collections from each would be redundant). So if one estimates an average clone size (perhaps 30 ft or less), and collects from plants *at least* this distance apart, there is reasonable assurance that one is collecting from different clones. Given the available information on pattern of genetic diversity, even adjacent (but not connected by rhizomes) plants can be collected with less concern that they are close relatives.

Example 2: *Danthonia spicata* (L.) Beauv. Ex Roemer & J.A. Schultes (Poverty oatgrass)

Figure 11.2. Poverty oatrass (*Danthonia spicata*). USDA-NRCS PLANTS Database / Hitchcock, A.S. (rev. A. Chase). 1950. *Manual of the grasses of the United States***.** USDA Misc. Publ. No. 200. Washington, DC.

1. In this hypothetical example, the main goal of the revegetation project is to restore ecosystem functioning and native plant diversity at all levels. There are no other major project objectives and so we skip to Step 3. The site has experienced two fires within the last few years. The second fire damaged regrowth on some species that sprouted after the first fire and removed the vegetation that had germinated from soil seed banks. Poverty oatgrass is a widespread perennial species, present in all states in Region 2 except Nebraska (Table 10.1).
2. Step 2 is skipped.
3. Although this species has been shown to increase after fires and can vegetatively reproduce, for this exercise it will be assumed that natural regeneration could be insufficient for recovery of this species on this site. Contributing rationale are that: the fire was very hot with complete coverage and there was a second fire that would have damaged some of the regrowth from the first fire. However, in many cases it may be assumed that natural regeneration would be sufficient and the decision-making process (for introducing more plants of this species) would end at this step.
4. The species is not listed as threatened or endangered on State or federal lists (Box 12).
5. There are no seed transfer rules available for this species.
6. This species is listed as being capable of vegetative reproduction (Table 10.2, Chapter 10). However, not all clones would necessarily survive (as noted in the Michigan study), so genetic diversity may be reduced.
7. There is a limited amount of genetic information available (Table 10.3). One study suggests that there is a fair amount of phenotypic plasticity (that is, the variation seen is related to environmental effects). Variation has been noted among populations in the mating system (that is, relative amounts of outcrossing versus selfing).

8. This species is not included among those with variable ploidy levels (Table 10.4, Chapter 10), nor are any other species in this genus listed as having variable ploidy levels.
9. The species has a mixed mating system. In one study that investigated inbreeding depression by comparing survival of plants from seeds of open (chasmogamous) flowers with closed (cleistogamous) flowers, differences were insignificant. This does not mean that the species might not suffer from inbreeding depression under some circumstances, but there is no evidence to date (Table 10.5, Chapter 10).
10. The site has not been disturbed other than by the two recent fires. There are other populations of this species within 50 km (30 miles). The soil A-horizon could have been affected by the fires: this is a consideration as to whether poverty oatgrass is now a reasonable species for the successional stage and site conditions.

Comments: There are no issues of multiple ploidy or inbreeding or outbreeding depression. There is little information available on local adaptation, or the spatial scale on which it might occur. One study suggests considerable phenotypic plasticity in the species. Furthermore, there is probably some natural regeneration after the fires. As such, the focus here is on supplementing (in the event some genetic diversity has been lost) and complementing the remaining genetic sources on site. Note that this is a hypothetical example: usually, poverty oatgrass would survive fire just fine, germinating from soil seed banks.

Example 3: *Sphaeralcea coccinea* (Nutt.) Rydg. (scarlet globemallow)

Figure 11.3. Scarlet globemallow (*Sphaeralcea coccinea*). Margaret Williams @ USDA-NRCS PLANTS Database.

1. In this hypothetical example, a large-scale fire has removed much of the vegetation, including one of the main nonwoody perennials, scarlet globemallow. The main goal of the revegetation project is to restore ecosystem functioning and native plant diversity at all levels. There are no other major project objectives and so we skip to step 3.
2. Step 2 is skipped.

3. There is some capacity for natural regeneration after a fire for this species: there can be a persistent soil seed bank and the species can also reproduce asexually via rhizomes. It is described as a pioneer species. Tentatively, the process is stopped here: there seem to be sufficient indications that the species may be able to regenerate sufficiently without assistance (Tables 10.1, 10.2).
4. The species is not listed as protected on the federal list or on any state list in Region 2 (Box 12).
5. There are no seed transfer rules available for this species.
6. Scarlet globemallow can spread vegetatively after a disturbance (Table 10.2, Chapter 10). No information is available on clone sizes.
7. Results from a rangewide common garden study suggest that there could be population-level differences in growth, possibly suggesting adaptive differences at that spatial scale (Table 10.3).
8. This species is not known to have various ploidy levels (Table 10.4).
9. Little information is available on the breeding or mating system, or for other species in the same genus. Self-sterility is common. Seeds are distributed mainly by gravity, with some secondary animal dispersal. This species is insect-pollinated (Table 10.1).
10. The site has not been disturbed other than by a recent fire.

Comments: There is little genetic information available for this species or information in its mating or breeding system. If there are not other issues, and especially if there are other populations of this species not far away, it may be best to allow some time to determine if the species can be re-established by natural regeneration. This choice is also supported by the potential of the species for some vegetative growth/spread after a disturbance and possibility of a persistent soil seed bank. If regeneration assistance is required, the appropriate subspecies should be selected (there are two described), and the closest populations chosen for seed sources. The role of insects in its pollen dispersal may indicate that it has more local spatial genetic structure than if it were mainly wind-pollinated.

Resources

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Chapter 12

Concluding Remarks

Genetic diversity and the environments which shape it are dynamic. Genetic diversity changes over space—both randomly and in response to the environment—and over time. It changes in response to both natural processes and to land management practices. In nature, each generation of plants is somewhat different from the parents. This means that defining an appropriate genetic source is a challenge because it is a moving target, and because genetic diversity is more often distributed as a continuum rather than discrete types that we can easily select and install appropriately. This fuzziness and the high levels of genetic diversity in many plant species often work in our favor, buffering our imperfect knowledge of the genetic landscape.

But the fuzzy genetic blueprint of most plant species should not discourage us from making decisions informed by the species' biology or genetic principles. If we err too far in our planting decisions, the consequences can be damaging not only to that particular project but have more widespread and long-term ecological consequences. Of course, maintenance of the genetic integrity of both native plant species and the species with which they interact will not be the main objective driving many revegetation decisions. Nevertheless, because local adaptation and ecosystem functioning may become a more important consideration for the site in the future, and because it is very difficult or impossible to rein in genes after they have been released on a site, it is still reasonable to consider genetics.

The importance of planning ahead is a well-established principle in land management. And it is particularly well applied in the discipline of choosing genetically appropriate sources for revegetating a site. Ideally, there is either a sufficient soil seed bank or remaining plants to allow natural regeneration. Some disturbances—depending on their severity and the biology of individual species—may remove or severely deplete the genetic resources on site. In that case, the genetic principles and information presented in this guide should assist in determining where best to collect genetic materials for the site. However, in some cases, either limited time or other circumstances may require that commercially available plant materials, including cultivars, be used. In that case, it is particularly important to be careful about the choice of plant material—its genetic source, and method of increase, if used. If genetic materials cannot be collected directly for a project, seeds that have been officially documented or certified as to source (that is, source-identified materials) are the next best choice. Uncertain identity of genetic materials introduces considerable risk into the revegetation decision. Many of these principles and practices are already familiar and routinely applied for commercially significant forest tree species: it makes sense to use similar considerations for other plant species when the management objectives are more inclusive.

With all of the information presented here on how to make appropriate genetic choices for revegetation materials, the management option of natural regeneration may be overlooked. Natural or unassisted regeneration (doing “nothing”) is often the best choice for maintaining genetic integrity. If there are sufficient genetic sources on site for the next generation (in the form of parent plants or soil seed bank, for example), natural regeneration bypasses the risks associated with introducing plants. In some cases, natural regeneration may not be practical or desirable, and occasionally it may not be the best option for genetic integrity of the plant species. In those relatively rare situations where there has been significant genetic erosion, introducing additional genetic diversity may be advantageous. But if plant populations (or plant parent materials remaining on site) are not suffering from genetic erosion, or if the added genetic diversity is too foreign, then there may be more harm than good done by the introduction. Within the context of managing the National Forests and Grasslands, more genetic diversity is not necessarily better. Moreover, even planting a non-invasive non-persistent exotic species may sometimes be a more ecologically compatible solution than planting an inappropriate genetic source of a local native plant species, and avoids the problem of genetic contamination.

Record-keeping is an essential companion activity to planning for good genetic management. Records of the genetic source of materials for past planting projects will help inform decisions about where to make new collections of seed materials. For example, one would avoid areas that had been planted with cultivars or unknown-source materials. Such records for current planting projects will be useful references in the future, allowing lessons to be learned as the planting matures. If there are problems with the planting, records of genetic source can help confirm or rule out a genetic component to the problem, and thus more clearly point to appropriate management tools to improve the situation.

Considerable information has been provided here on the different types of genetic information and different methods to assess genetic diversity. This topic may be beyond the interest of some readers. However, there are a few key points that can be teased from all the descriptions of DNA from different organelles and different types of analysis, and they can be simply stated. First, there is more than one way to measure genetic diversity. Second, the most appropriate method will depend on what question you want to ask. Third, all the numbers or statistics that are used to quantify genetic diversity require an appropriate context for interpretation: they mean little on their own. Finally, different measures of genetic diversity may appear to give conflicting results for a species, but this isn’t the case. Rather, they reflect different kinds of genetic diversity or different influences and so are telling different parts of the story.

Guidelines have been offered here for making decisions about the most appropriate genetic materials for revegetation projects when a major goal is that of protecting biodiversity, including genetic diversity. The guidelines have been organized around individual species, and a step-wise consideration of various traits and types of genetic information that may be available. This is a different, although complementary, approach to that of constructing discrete or continuous seed zones (including continuous seed zones). Considerable amounts of information on adaptive genetic diversity are required for development of valid seed zones for each species. The guidelines provide a means of making use of more modest amounts of information about a species, to inform the decision as much as possible even when seed zone information is lacking. By basing our guidelines on individual species, a different spatial scale for determining what is ‘genetically local’ can be applied to each species. The guidelines appropriately recognize that one spatial scale or one definition of “genetically local” will not ordinarily apply to other species.

Ideally, there would be a comprehensive understanding of the genetic diversity of every native plant species. However, this is unrealistic to expect in the near future, if ever. In cases where genetic information that is relevant to revegetation decisions is available, it should be appropriately interpreted and applied. However, in the absence of this direct genetic information, correlated features may provide some guidance about the genetic nature of the species. We have emphasized the relationships between patterns of genetic diversity and plant characteristics such as their mode of reproduction, breeding system, and means of seed and pollen dispersal. For example, species that are largely selfing or frequently reproduce by vegetative (non-sexual) means often have stronger among-population genetic differentiation among their populations than outcrossing or sexually reproducing species. This generalization would guide the manager towards selecting revegetation materials for that species only from the same or very local populations (depending on how the species was spatially structured), if possible. In contrast, when compared over similar spatial distances, long-lived, outcrossing, wind-pollinated plant species frequently have more modest genetic differentiation among populations—a generalization that is consistent with gene flow that tends to unite populations through the longer reach of pollen dispersal in these species. For species with those characteristics, there may be a broader range of “appropriate” sources of genetic materials for revegetation of a particular site.

Selecting appropriate species for revegetating a site is a familiar process for land managers. We now recognize the often dramatic consequences of making an inappropriate decision, such as exotic species becoming established or failure of the installed plants if they are not well matched to the site. Here, we have presented the case that there is actually a continuum of plant diversity from plant communities to species to populations to individuals to DNA. Genetic diversity is one part—a critical part—of biological diversity. In that context, the decision of which native species to plant is bracketed by two companion questions: how does this species fit within the plant community and what part of that species is native to the local area?

This Guide helps to address this second question so that science-based choices can be made: determining what subspecies, ecotype, cytotype, population, or other subset of a plant species is appropriate to the genetic and ecological landscape of interest. Often, this decision is not straightforward, but can be informed by scientific information. As the decision of the appropriate genetic source for plant material will often require discretion, this Guide has included substantial information on the nature, significance, and assessment of genetic diversity. When specific genetic information on a plant species is lacking, this enhanced understanding of genetic diversity, coupled with some modest knowledge of the species’ reproductive characteristics, will provide a reasonable basis for selecting appropriate germplasm.

As a prominent land-managing agency, the Forest Service has a long history of managing natural resources and making complicated decisions. The agency also has a history of leadership in conducting the research and establishing the field trials that have provided much scientific information that is useful in these decisions. Recognizing that scientific information is often not the only consideration in making management decisions for natural resources, there has nevertheless been a longstanding commitment to appropriately incorporating the science that is relevant to the particular decision. The sophistication of this process within the Forest Service continues to grow with its ongoing investments in scientific research and the development of decision tools such as the “science consistency review”—a process to determine whether an analysis or decision document is consistent with the best available science (Gulden et al. 2003). In keeping with this tradition of valuing the role of scientific information in making decisions that affect our natural resources, this Practical Guide is intended to make genetic information more accessible to land managers by determining the most relevant information, presenting this information in one location, interpreting the literature, and providing alternative types of information to consider when genetic information is lacking or insufficient.

Literature

Gulden, J.M., D. Cawrse, R. Graham, M. Hemstrom, L. Joyce, S. Kessler, R. McNair, G. Peterson, C.G. Shaw, P. Stine, M. Twery, and J. Walter. 2003. Science Consistency Reviews: A Primer for Application. USDA Forest Service FS-771, 9 p.

Glossary

This glossary contains some of the more technical words used in the chapters and boxes in this Guide. The intent is to provide a brief definition that provides sufficient clarity for the Reader to understand the term in the context in which it was provided in the text. If a word appears only once in the Guide, or perhaps in only one chapter, it is defined where it is used and may not appear in this Glossary. Many words have a broader or more detailed description that is beyond the scope of this Guide; we have tried to present the information or aspect of the term that is most relevant to this Guide's use. Terms that are used, for example, in the context of tree improvement, conservation biology, and population genetics may have slightly different interpretations in each of those contexts. Some assistance with definitions was gained from the references listed at the end of the glossary.

Adaptation: The result of repeating cycles of reproduction and selection such that, over time, the traits that are better suited to the environment increase in relative frequency or intensity (assuming they have a genetic basis). Adaptation occurs over time and acts at the level of the population. An individual does not adapt. Often the change in the trait structure or function is referred to as an adaptation.

Adaptive strategy: Several traits that, in combination, confer an advantage to the species or organism in its environment.

Adaptive variation: That portion of the total genetic diversity that underlies traits that are adapted to the environment.

Additive genetic variation: Genetic variation associated with the average effects of substituting one allele for another.

AFLP: Amplified fragment length polymorphism. A diagnostic DNA fingerprinting technique that detects restriction fragments, similar to RFLP, but for which polymerase chain reaction (PCR) is used to replicate to amplify the DNA fragments to provide a suitable amount.

Agamospermy: A type of asexual reproduction in plants in which viable seeds are produced without pollination or other means of genetic recombination (though mutations are possible); one type within the broader category of apomixis.

Aggressiveness: Seedling vigor related to ease of establishment. Also, capacity of well-established plants to compete with or out-compete associated grasses, legumes, or woody plant species.

Allele: One of two or more forms of a gene; more accurately, one of two or more forms that can exist at a single gene locus (place on the DNA).

Allopolyploid: A polyploid containing multiple sets of chromosomes derived (originally, during its evolutionary history) from two or more species. That is, the origin of the species involved hybridization of different species at some point in the past, as opposed to simple duplication or replication of the chromosome set of one species. From the Greek ‘allos’ (other).

Allotetraploid: A polyploidy species that evolved from hybridization between two different species, and having four sets of chromosomes.

Allozyme: One of several forms of an enzyme coded for by different alleles at a locus. Enzymes are a class of proteins that function as catalysts in metabolic reactions. Allozymes differ from one another due to small changes in the genetic code that result in changes in the amino acid building blocks that result in proteins with differing folding structure, size, or electrical charges. These attributes cause the different allozymes to migrate different distances across an electrical current within an electrophoretic gel. In most cases, these structural and mobility differences do not translate into detectable functional differences. Such variation is said to be ‘neutral’. Sometimes the different allozymes do affect the relative performance of individual plants in nature, and in such instances, the variation is said to be ‘adaptive’ rather than neutral.

Amphidiploid: A collective term meant to cover all types of polyploids which have arisen after hybridization between two or more diploid species.

Aneuploid: An organism that has an imbalance in its chromosome sets; the chromosome number in its body cells (for example, diploid) is not an even multiple (in this case, 2x) of its haploid number (the number of chromosomes in pollen cells).

AOSCA: Association of Official Seed Certifying Agencies.

APHIS: Animal and Plant Health Inspection Service of the US Department of Agriculture.

Apomixis: A general term, encompassing all types of asexual reproduction, resulting in normal (for example, diploid); offspring without the fusion of gametes; includes agamospermy (asexual reproduction by means of seeds) and other types of asexual reproduction including bulbs, bulbils, runner, and layering.

Artificial selection: Intentional selection (by people, as opposed to natural selection) of individual plants from a broader array (such as a provenance or family) having the best characteristics for a particular use.

Autogamous: Plants that are obligatory self-fertilizers.

Autotetraploid: A tetraploid population (or species) derived by combining the chromosome sets of two diploid populations of the same species. Could be the condition for the entire species if this event happened historically and the other diploid populations did not persist.

Backcross: The crossing of a hybrid with either of its parents.

BAER: Burn Area Emergency Rehabilitation. A program of the USDA Forest Service for the purpose of providing policy and improving procedures for assessment and implementation of appropriate measures for emergency watershed rehabilitation after wildfires to minimize threats to life and property, protect the quality and stability of the water supply, and reduce the loss of soil and onsite productivity. See BAER Handbook FSH 2509.13.

Biodiversity: Refers to biota in terms of taxonomic and genetic diversity, the variety of life forms present and the community structure thereby created, and the ecological roles and processes performed. There are four levels to biodiversity as defined by USFS—landscape, ecosystem, species, and genetic diversity.

Blend (= Seed blend) A mixture of seed of known proportions of two or more lots, or variation of the same species.

Breeder seed: Seed or vegetative propagating material which is directly controlled by the originating or, in some cases, the sponsoring plant breeder, institution, or firm, and which supplies the source for initial and recurring increase of foundation seed.

Breeding zone: A geographic area based on anticipated adaptability of an improved population of trees. A geographic area of similarly adapted trees within a species for a specified range of elevations, generally based on patterns of genetic variation for adapted traits. The breeding zone is a geographic-elevational subdivision where it is presumed that no serious problem will result from genotype-by-environmental interactions.

Canopy seed bank: Seeds that are held—typically in cones—in the canopy of trees. Often refers to a situation where seed-containing cones may be held in the canopy for many years before being released (such as in cones of certain pines or other species that open in response to fire). serotinous or semi-serotinous cones).

Certified seed: Seed that is handled in ways which maintain satisfactory genetic identity and purity and that has been approved and certified by the certifying agency. Certified tree seed is defined as seed from trees of proven genetic superiority, as defined by the certifying agency, produced so as to assure genetic identity.

Chloroplast: Organelle within a plant cell that contains chlorophyll; the site where photosynthesis takes place; one of three organelles in plant cells (along with nuclei and mitochondria) that contains DNA.

Chromosome: Structural unit within the nucleus of a cell that bear the genes.

Cleistogamy: Designating a plant that produces inconspicuous self-pollinated flowers that never open.

Cline: A geographical gradient in a characteristic of a plant within the species' range. Often clinal variation results from an environmental gradient, such as elevation.

Co-adaptation: The process of selection by which harmoniously interacting genes become accumulated in the gene pool of a population.

Co-adapted gene complexes: A group of genes (often, but not necessarily, in close proximity on a chromosome) which tend to be inherited as a group that interact to form a beneficial effect to the organism and are favored over time through natural selection.

Coding sequence: A sequence of DNA that contains the information to form a polypeptide; that part of a gene that is expressed.

Co-dominance: The relationship between pairs of alleles such that each contributes towards the product or trait; more generally, heterozygous offspring have characteristics of both parents (for traits that have a genetic basis that is co-dominant.)

Commercial seed: Seed produced by commercial industry; may or may not be recognized improved varieties of seed.

Common-garden study: A test that provides a uniform environment in which different individuals within a species can be grown and compared to detect genetic variation. Differences observed across a species' range may disappear when individuals from those areas are grown under uniform conditions.

Cryopreservation: Storage at ultra-low temperature, usually that of liquid nitrogen (-196 degrees C.). At such low temperatures, all cellular processes are stopped and the plant material can theoretically be stored (without alteration) for a long time.

Cultivar: An assemblage of cultivated plants that is clearly distinguished by morphological, physiological, cytological, chemical, or other traits, and when reproduced (sexually or asexually), retains its distinguishing characters. The term is derived from 'cultivated variety'. For cultivated plants**,** the term cultivar is the equivalent of a botanical variety, in accordance with the International Code of Nomenclature of Cultivated Plants 1980. Cultivar names are denoted with single quotation marks or by saying it is a cultivar.

Cytotype: Any variety or population of a species whose basic set of chromosomes differs quantitatively or qualitatively from the standard of that species. For example, if a species is polyploidy, and some populations are composed of diploid plants and other populations are composed of tetraploids, the species would be said to have two cytotypes.

Dominance: The type of relationship between pairs of alleles such that one allele masks the other; an individual that is heterozygous for a trait controlled by these alleles would be similar to an individual that had two of the same (dominant) alleles but different from an individual that had two of the masked (recessive) alleles.

Dioecious: Possessing male and female flowers or other reproductive organs on separate, unisexual, individual plants. Derived from the Greek term *okios* (housed), therefore 'in two houses'.

Diploid: Having a pair of each chromosome.

Directional selection: When selection favors one end of a range of phenotypes. If the phenotypes are genetically controlled, the result is a shift in typical phenotype toward the favored value (e.g., flower color).

Disomic inheritance: The condition of having a pair of chromosomes of the same kind inherited from one parent (as may occur in polyploidy species). The alternative (standard) condition is heterodisomy, where one member of each chromosomal pair is inherited from each of two parents.

Disruptive (or diversifying) selection: When selection favors phenotypes on two ends of the distribution of phenotypes. If the phenotypes are genetically controlled, the result is diversification of populations.

District Seed Increase (DSI)**:** Foundation seed from a Plant Materials Center provided through a conservation district to a district cooperator for the increase of that seed. Commonly used for new releases to speed the availability of seed on the commercial market.

Dormancy: An internal condition of the chemistry or stage of development of a viable seed that prevents its germination, although temperature and moisture are adequate for growth; also, can apply to a living plant that is not actively growing aerial shoots or roots.

Ecological race: Group of local populations within a species in which individuals have similar environmental tolerances that differ from those for the rest of the species. Wide-ranging species may consist of many ecological races.

Ecoregion: A general region, variously defined, that shares some common ecological characteristics often in combination with certain environmental features (such as temperate forest, desert savannah).

Ecotone: Transitional zone between two vegetational types or regions. A transition area of vegetation between two plant communities, having characteristics of both kinds of neighboring vegetation as well as characteristics of its own. Width varies depending on site and climatic factors. Ecotones are necessarily dynamic in composition and position.

Ecotype: A race of plants whose characteristics are adapted to a distinct habitat. Some differences among ecotypes, particularly those wholly physiological, show up only when plants from different ecotypes are grown in a single environment. Ecotypes are described as climatic, edaphic, etc. The observed relationship between the characteristic and the environment is discrete rather than continuous.

Ecotypic differentiation: Ability of a species to develop local populations genetically appropriate for varying environments.

Ecovar: The offspring of native species that have been developed from original plant material collected from a specific ecological region. Selection is done with minor emphasis on improving agronomic characteristics and major emphasis on maintaining genetic diversity.

Effective population size (N_e): The size of an ideal population whose genetic composition is influenced by random processes in the same way as the real population. The effective population size—a reflection of the size of a population as measured in genetic terms—is often considerably smaller than its census size. Also, a measure of the number of individuals in a population that contribute genes to succeeding generations.

Endemic: A native species that is restricted to a well-defined and often-small area. This is a relative term and is used in conjunction with the area to which its total natural range is confined (for example, a state, county, or geographic area). For example, ‘endemic to Colorado’ means that it is native only to Colorado. If the species was also found naturally in Wyoming, it would not be correct to say that it is endemic to either Colorado or Wyoming, but native to both.

Epistasis: An effect on the phenotype of an individual (for example, its size) that is the result of the combined interaction of two or more gene loci and is different from the effect of each locus operating individually.

Evolve: The long-term process by which species arise and become extinct; change in the genetic composition of a population.

Exotic species: Introduced from a foreign place, typically a different country. Sometimes also used to described far-ranging populations of a species that is native to more than one country.

Ex situ: Off site, away from the place to which it occurs naturally.

***Ex situ* collection**: A collection (in this case, of plant genetic material) that is maintained outside of its natural habitat, such as seed collections, seed orchards, arboreta, and so on.

Extinction: No individuals of a pre-existing species survive. This has various caveats such as ‘extinct in the wild’ when the only remaining individuals or seeds occur in arboreta, nurseries, or seedbanks, but no longer in nature; also used in other contexts such as ‘local extinctions’ (extirpation), and extinction at other genetic levels (such as genes, genotypes, and so on).

Extirpation: Local extinction, often of populations of a species. Whereas a species becomes extinct when all of its members are gone, when the species ceases to exist in former parts of its range, or has lost some populations, those losses are ‘extirpations’.

Fitness: The average contribution of one allele (one form of a gene) or genotype to the next (or succeeding) generation(s) compared with that of other alleles or genotypes to obtain relative fitness. Also, Darwinian fitness: The relative probability of survival and reproduction for a genotype.

Foundation seed: The progeny of breeder seed that is so handled as to most nearly maintain specific genetic identity and purity. Production may be carefully supervised by the originating agency and approved by the certifying agency, the agricultural experiment station, or both.

Gene bank: An establishment in which both somatic and hereditary genetic material are conserved (seeds, pollen, whole plants, extracted DNA) in a viable form. The stored material can be accessed and used as appropriate.

Genecology: The study of how genotype controls responses of populations to habitats.

Gene flow: Movement of alleles between populations due to migration of individuals (such as seeds) or pollen distribution; also called gene migration or genetic migration.

Gene pool: The totality of the genes of a given (sexually reproducing) population.

Genetic architecture: The underlying genetic basis of a phenotype, including additive and interaction effects within and among genes gene loci, and how they are modulated by the environment. (Sometimes also used to refer to the genetic structure and genetic diversity attributes of populations, but this confuses the original intended meaning.)

Genetic assimilation: A process of hybridization and subsequent backcrossing between two populations or related species that ends with one becoming genetically similar to, and hence replaced by, the other.

Genetic bottleneck (or bottleneck): A restriction in population size that is sufficiently severe and longlasting that it causes a loss in genetic diversity.

Genetic contamination: Introduction of foreign or nonlocal alleles or genetic diversity into a population. Often more narrowly interpreted to include only detrimental introductions that demonstrably or potentially undermine local adaptations.

Genetic differentiation: A quantitative expression of genetic differences, often among populations. Measured by various statistics, often F_{ST}.

Genetic diversity: That part of the total (phenotypic) variation in a population or species that is genetically based.

Genetic integrity: As defined here, refers to the quality and arrangement of genetic diversity—within individuals and across the landscape—in relation to natural processes. It thus reflects changes in genetic composition caused by local natural selection and other processes that can influence the mating success and survival of individuals.

Genetic structure (also ‘spatial genetic structure’): Referring to the spatial pattern of genetic diversity within a species, such as how genetic diversity is distributed among and within populations.

Genetically local: Plant materials that reflect the amount and type of genetic diversity that is typical for a particular plant species in the area under consideration.

Genome: The total genetic information carried by a single set of chromosomes in a haploid nucleus.

Genotoxic: Substances that can cause damage to DNA.

Genotype: An individual’s hereditary constitution, expressed or hidden, underlying one or more characters; the gene classification of this constitution expressed in a formula. The genotype is determined chiefly from breeding behavior and ancestry. It reacts with the environment to produce the phenotype.

Genotype x environment interaction (= genotype by environment interaction): A different type of response to a change in environmental conditions by different genotypes. In common-garden tests, for example, this is represented by a change in the performance ranking of given genotypes when grown in different environments.

Geographic race: A subgroup of a species that is restricted to a geographical area. This does not necessarily imply local adaptation.

Germplasm: The genetic material of a species; the hereditary material transmitted to offspring through the germ cells; in plants, includes DNA in the nucleus, mitochondria, and chloroplasts.

Haploid: A complete single set of chromosomes (such as that found in the egg cells or pollen).

Haplotype: Alleles from a sequence of linked genes from a single chromosome. Diploid individuals have two haplotypes for a given segment of DNA. The term can also apply to a DNA sequence that includes a gene and its adjacent regions.

Heterozygosity: The presence of different alleles (types of a gene) at matching locations on a chromosome pair.

Heterosis: The increase in mean fitness of a first-generation hybrid population of F1 progeny relative to the average of the two parental populations. Also called hybrid vigor.

Homozygosity: The presence of identical alleles for a particular gene on both (or all, in the case of a polyploidy) matching chromosomes; no genetic variation for the gene in that individual.

Hybridization: A cross between genetically different individuals that could be from the same population, different populations (both instances of ‘intraspecific hybridization’), or from different species (interspecific hybridization).

Increase plantings (= seed increase): Production of seed or other reproductive parts of plant material to be made available for use in evaluations, field plantings, demonstration plantings, educational plantings, or for distribution.

Initial increase: The production of small quantities of seed or other reproductive parts of plants selected from initial or advanced evaluations to be used for further evaluation and exchange.

In situ: On site (as opposed to off-site or ex situ). Often used to describe a conservation strategy in which organisms are protected in their native environments (in situ) in contrast to being stored off-site (ex situ conservation).

Invasion: The migration of organisms from one area to another area and their establishment in the latter.

Invasive species: A species that invades habitats, demonstrates rapid growth and spread, and displaces other species. Species that are prolific seed producers, have high seed germination rates, easily propagate asexually by root or stem fragments, and/or rapidly mature may be predisposed to become invasive. Also, Executive Order 13112 (1999) and the National Invasive Species Management Plan (2001) both define invasive species as "… an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health."

Isolation by distance: A model, or actual spatial genetic pattern, in which individuals closer together are more genetically similar than those further away.

Isozyme (=isoenzyme): Enzyme product coded for at a specific location on the chromosome. See also glossary definition of allozyme.

Layering: A type of vegetative (asexual) reproduction in which covering stems, runners, or stolons with soil causes roots to form at nodes; can occur in nature in some plants and is also sometimes used as a propagation technique in horticulture.

Life-history trait: Development traits for a particular species or population such as age or size at first reproduction, number of offspring per reproductive episode, annual or perennial or biennial; More generally, characteristics that are typical for a particular species such as its breeding system, taxonomic status, type of seed dispersal, or reproductive method.

Local population: Group of individuals of the same species growing near enough to each other to interbreed and exchange genes.

Local seed source: Any part of a geographic area where seed may be collected which is demonstrably or presumably from the geographic race native to a designated site.

Major Land Resource Areas (MLRA)**:** A system of land classification composed of geographically associated land resource units; MLRAs are important in agricultural and other types of regional planning. Land resource units are geographic areas, usually several thousand acres in extent, that are characterized by a particular pattern of soils, climate, water resources and land uses.

Maladaptation: When an individual lacks the specific genetic material needed to be adapted to a site.

Mass selection: Selection of individual plants and propagation of the next generation from the aggregates of that seed.

Microsatellite: DNA (deoxyribonucleic acid) contains many repeating sequences of genetic code, most of which doesn't lead to the production of anything (as far as we know). Microsatellites are clusters of repeating segments. Each segment includes about two to five basic units (nucleotides), and each cluster includes about 10-20 such segments. They are highly variable, numerous, and scattered throughout a pair of chromosomes. Occasionally microsatellite variation is adaptive.

Migration: Movement of individuals (for example, seeds) between populations; in the context of population genetics theory, this is also used as a synonym for gene flow among populations.

Mitochondria: Structures within cells that are the major site for energy production; one of the three cellular structures in plants that contains DNA.

Monoecious: Possessing separate male and female flowers on the same individual plant.

Native species: A native plant species is one that occurs naturally in a particular region, state, ecosystem, and habitat without direct or indirect human actions. Climate, soil, and biotic factors determine its presence and evolution in an area.

Native species: One that occurs naturally in a particular region, state, ecosystem, and habitat without direct or indirect human actions. Its presence and evolution in a given area are influenced by climate, soil, and biotic factors.

Naturalized species: A species introduced from another area that has become established in and more-or-less adapted to a region by long, continued presence there; does not require artificial inputs for survival and reproduction, and has established a stable or expanding population. Examples: cheatgrass, starling.

Natural selection: The differential survival or reproductive success of different genetically based phenotypes.

Non-native: A plant grown outside its natural range; includes exotics.

Noxious species: A plant species that is undesirable because it conflicts, restricts, or otherwise causes problems under management objectives. If declared noxious by law, this is called a noxious weed.

Nucleus: The membrane-bound organelle (in cells) that contains the chromosomes; one of three organelles in plant cells that contains DNA.

Nurse crop: Plants that are installed on a site prior to or coincident with the (different) intended species so as to create growing conditions that are more favorable for the intended species.

Outbreeding depression: A reduction in reproductive fitness due to crossing of two populations that differ from each other; the mean fitness of the cross (offspring) is less than the mean of the parents.

Outcrossing: A mating system in which successful fertilization from non-relatives is favored or more likely than that with relatives or self-fertilization.

PCR: Polymerase chain reaction. Technique used to replicate fragments of DNA. The process allows even small amounts of DNA to be used for genetic analysis.

Perfect flowers: Having both functional pistils and stamens.

Phenology: A branch of science dealing with the relationship between climate and periodic biological phenomena. Also dates or sequence of occurrence of different growth stages of plants.

Phenotype: The observable manifestation of a specific genotype. That is, those properties of an organism, produced by the genotype in conjunction with the environment.

Phenotypic plasticity (plastic genotype): Wide range of character expression (phenotypic response) of a given genotype. For example, if different copies of a clone (such as rooted cuttings taken from a quaking aspen) are grown in different environments, the different growth rates, leaf sizes, or branch angles seen in the different trees are expressions of plasticity.

Photoperiod: The relative lengths of the periods of light and darkness associated with day and night.

Ploidy: The number of complete chromosome sets in the cell nucleus (such as diploid, tetraploid, and so on).

Polycross: In tree improvement, a cross between one plant acting as the female and a mixture of pollen from several to many males, such that the paternal contribution to the progeny is unknown. This mating design is used to estimate various measures of the value of the female parent (for example, heritability, breeding value) for the traits of interest.

Polyploid: Possessing more than two complete chromosome sets; that is, having more chromosome sets than a diploid.

Population: Technically, it is a group of interbreeding individuals. However, with plants, pollen dispersal may be far-reaching, inconsistently distributed over time, or otherwise difficult to track making this definition impractical or difficult to apply. Commonly used to describe a geographically discrete or otherwise identifiable group of plants within the species.

Population genetics: The study of genetic principles (such as Mendel’s laws) as they apply to entire populations of organisms.

Population viability: The long-term likelihood of persistence of a population.

Post-fertilization incompatibility: Genetically determined inability to form viable seeds following fertilization. Incompatibility could be to self-pollination or crossing with certain other plants.

Pre-fertilization incompatibility: Genetically determined inability to obtain fertilization and seed formation.

Pre-varietal germplasm: Seed that has been certified but has not yet been that have not been selected as a variety for commercial release.

Progeny Test: 1) In testing for adaptation to particular environments, evaluation of selected individuals (parents) by comparing performance of their offspring (progeny). 2) In testing for effects of hybridization, evaluation of offspring from controlled crosses to determine the genetic basis of traits (genetic versus environmental control of phenotypic traits) and the effect of hybridization on fitness, including germination, survival, growth, and reproduction.

Propagule: Any form of plant tissues to be used for reproduction (such as a seed, seedling, bulb, tuber, root fragment, rooted or unrooted cutting, a graft, a tissue-cultured plantlet, and so on).

Provenance: The original geographic source of seed or propagules.

Provenance test: A field (or nursery) test in which seeds are collected from multiple populations, the seedlings grown in common environments, and the genetic variation observed for various of traits reflecting either productivity or environmental adaptation.

Quantitative trait: Measurable traits such as size and reproductive rate that typically have continuous variation (as opposed to discrete categories) in a species. Variation of these traits is controlled by many genes and by environmental conditions.

Race: A population within a species which exhibits general similarities discontinuous and distinct from other populations though not sufficiently so to achieve the status of a taxon, (for example, a subspecies). When the distinguishing characteristics of a race are adaptive, the term is synonymous with ecotype, and the population in question is described similarly (relative to, for example, climate or soils).

RAPD: Random amplified polymorphic DNA. A procedure for detecting genetic diversity. It differs from some other methods (such as allozyme analysis) in that it is interpreted as presence/absence of dominant alleles only, and therefore, heterozygous loci can’t be distinguished from homozygous dominant loci.

Ramet: An unrooted cutting; a member of a clone.

Random genetic drift: Changes in the genetic composition of a population due to random survival (from one generation to the next) not based on environmental fitness, particularly in small populations. It can result in loss of genetic diversity and changes in allele frequencies. Frequently referred to as genetic drift.

Reciprocal cross: A second cross involving the same parents as the first but with the sex of the parents interchanged.

Reclamation: The salvage of severely degraded land such as old mine sites to a condition that supports plant life. The goal may fall far short of providing a functioning natural ecosystem depending on goals, plausibility, and context. For example, the project site may be so degraded that return to a self-supporting native ecosystem is highly unlikely. Project goals may range from self-sustaining native ecosystems to managed landscapes of non-native plants.

Recurrent selection: A method of breeding designed to concentrate favorable genes scattered among a number of individuals by selecting in each generation among the progeny produced by inter-mating of the selected individuals of the previous generation.

Refugia: Locations in which species have persisted, while becoming extinct in other locations. This is often in the context of evolutionary time and in response to major climatic events such as glaciations.

Registered seed: The progeny of Foundation seed that is so handled as to maintain satisfactory genetic identity and purity and that has been approved and certified by an appropriate agency. This class of seed should be of a quality suitable for production of certified seed.

Registered variety: (1) For grasses and agricultural species: A variety accepted, numbered, and registered as a recognized improved variety by the Committee on Varietal Standardization and Registration of the Crop Science Society of America. (2) For other species: A variety, which has been registered with the appropriate International Species Registrar.

Regression: A statistical analysis examining pairs of variables for a relationship between the variables. For example, a regression analysis can determine how well the first date of flower opening (independent variable) predicts the number of seeds produced (dependent variable) by different genotypes in a particular environment. Determination of an actual cause-and-effect relationship between variables must be tested experimentally.

Rehabilitation: Modification of degraded ecosystems or disturbed areas to assist return to a functional condition. As in restoration, rehabilitation may involve revegetation, replacement or removal of invasive species, changes in grazing practices, removal of domesticated grazing animals, return of natural fire intervals or other actions that increase the probability of return to a functional ecosystem. Postfire rehabilitation may be doing whatever it takes to stop or reduce soil erosion after fire by mechanical methods or by encouraging vegetative cover. The goal of rehabilitation emphasizes functionality, but it does not imply a return to a natural sustainable ecosystem.

Released plant material: Source-identified, tested, selected, or cultivar classes of plant material, or other germplasm for a conservation purpose that is made available to the public, according the standards set by the Experiment Station Committee on Organization and Policy (ESCOP). The different kinds of releases are defined by the Association of Official Seed Certifying Agencies (AOSCA) and in the US Federal Seed Act.

Released variety (= Released cultivar): A new variety/cultivar of proved value that is made available to the public, according to the Experiment Station Committee on Organization and Policy (ESCOP) standards, for a conservation purpose.

Reproductive fitness: The number of fertile offspring surviving to reproductive age contributed by an individual. Can be measured in absolute or relative terms.

Restoration (= ecological restoration): The process of assisting a disturbed or altered site by encouraging a trajectory toward a condition that emulates a previous natural condition.

Revegetation: A general term that refers to the reestablishment of plant cover through planting seeds or other plant resources such as cuttings, vegetative propagules, or containerized plants where there is currently little or no vegetation. Revegetation can be accomplished with cultivated, exotic, or native wild plants. There is no particular goal implied other than producing vegetative cover. Reclamation, rehabilitation, and restoration frequently involve revegetation.

RFLP: Restriction fragment length polymorphism. DNA sequence variation that is found by cutting DNA with certain types of enzymes, producing fragments of DNA of different lengths. The fragments are separated using electrophoresis. Various methods are then used to view the bands within the gel.

Translocation: Movement from one location to another; frequently refers to samples of populations that are introduced by people into a new location.

Scaling up: Increasing the number of plants (as seed, seedlings, or rooted cuttings) available from a limited set of parents or source materials. Those source materials could be increased through sexual (producing seeds) or asexual (cuttings) means.

Seed bank (facility): A place or storage area where seeds are kept, usually under cool conditions to maintain their viability and improve their shelf life. Also, soil seed bank refers to a collection of seeds that may persist in the soil for some species—from a few months to many years, depending on species and environmental condition.

Seed certification: A system whereby seed of plant cultivars (and pre-varietal releases) is produced, harvested and marketed under authorized regulation to insure seed of high quality and genetic purity.

Seed certification classes: Categories of seed produced by a grower to ensure the purity of the genetic material. Seed that undergoes the certification process is typically inspected during the growing season or at harvest and when the seed is tested. Certification classes include: Breeder, Foundation, Registered, Certified, and Common.

Seed Certifying Agency: General term for the state or other agency responsible for the release and certification of crop varieties and for inspecting and approving seed produced under one of the seed certification classes. Most seed certification agencies are members of the Association of Official Seed Certifying Agencies (AOSCA).

Seed collection zone (=seed zone): Area having defined boundaries and altitudinal limits within which soil and climate are sufficiently uniform to indicate high probability for maintaining a single subdivision of plants that are adapted to a specific set of environmental conditions.

Seed increase (also = increase plantings): Production of seed or other reproductive parts of plants to be made available for use in evaluations, field plantings, demonstration plantings, educational plantings or for distribution.

Seedlot: A definite quantity of seed identified by a lot number, every portion or bag of which is uniform, within permitted tolerances, for the factors that appear on the label. Examples include seed produced by open-pollination from a particular tree, seeds from one controlled cross, or seeds collected from a specific geographic area.

Seed purity: The percentage of the desired species in relation to the total quantity, including other species, weed seed, and foreign matter.

Seed source: Typically refers to the locality where a seed lot was collected. If the stand from which collections were made was from non-native ancestors, original seed source may be used to designate the original place of collection. Synonymous with geographic race, provided the latter has been demonstrated.

Seed tree: Individual trees or groups of trees intentionally left during a harvest operation to act as a source of seeds for regeneration.

Selected Class Release: Seed that is the progeny of rigidly selected seed or stands of untested parentage that has promise, but not proof, of genetic superiority, and for which geographic source and elevation shall be stated on the certification label.

Self-compatible: A plant that can be self-fertilized.

Self-incompatible: Controlled physiological barrier to self-fertilization; inability to set seed from application of pollen produced on the same plant. There are several mechanisms responsible for self-incompatibility in higher plants.

Self pollination: The transfer of pollen from the anther of a flower to the stigma of the same flower, or different flowers on the same plant.

Self-sterility: Unable to produce viable seed from self pollination.

Semelparous: Organisms that reproduce only once during their lifetime.

Sex ratio: The relative number of breeding males and females in a population, often expressed as a percentage—obtained by dividing the number of males by the number of females.

Single copy DNA: DNA sequences that occur once per haploid genome, as opposed to repetitive DNA that occurs in multiple copies.

Source-identified seed: Seed, seedlings, or other propagating materials collected from natural stands, seed production areas, seed fields, or orchards where no selection or testing of the parent population has been made.

Stabilizing selection (or normalizing selection): Selection favoring intermediate phenotypes. If the phenotypes are genetically determined, the result is a narrowing of the range of phenotypes. (See also disruptive selection and directional selection).

Subspecies: A class within a species used to describe geographically isolated or otherwise differentiated variants; a category above ‘variety’, indicated by the abbreviation ‘ssp.’ in the scientific name.

Succession (=ecological succession): A natural process occurring over long time periods in which changing conditions (both biotic and abiotic) favor different populations and species such that the biological composition of a site gradually changes. Species that are well-adapted to conditions that have little vegetation (for example, because of a recent disturbance) are often described as ‘early successional species’ and may have characteristics that include soil seedbanks or below-ground propagules, spread rapidly, and be light-tolerant or shade-intolerant.

Suckering: Producing vegetative shoots below ground that can give rise to new (but genetically identical) plants.

Synthetic variety: Advanced generation progenies of a number of clones or lines (or of hybrids among them) obtained by open-pollination.

Testcross: A cross between a heterozygote (for the gene of interest) of an (unknown) genotype and an (known) individual that is homozygous (for the recessive gene of interest) to learn more about the unknown genotype, through the resulting offspring; in general, any cross that contributes to the solution of an experimental question by using more or less defined crossing partners.

Tested Seed: (1) Seeds or plants which have been through additional testing on more than one generation which will include testing on multiple sites with replicated plots to verify performance and heritability of desirable traits. The material has proven genetic superiority or possesses distinctive traits for which heritability is stable as defined by the certifying agency. (2) One of the classes of pre-varietal releases recognized by AOSCA.

Tetraploid: An organism having four basic sets of chromosomes.

Topcross progeny: Progeny from outcrossed seed of selections, clones, or lines crossed with a single variety or line that serves as a common pollen parent.

Type: A group of varieties so nearly similar that the individual varieties cannot be clearly differentiated except under special conditions. For further information, refer to the Federal Seed Act Rules and Regulations

Transgene: A gene introduced into a host genome by biotechnological means.

Transgenic plant: A plant that contains an alien or modified DNA (gene) introduced by biotechnological means and which is more or less stably inherited.

Transposable element: A chromosomal locus that may be moved from one spot to another within and among the chromosomes of the genome; it happens through breakage on either side of these loci and their subsequent insertion into a new position either on the same or a different chromosome.

Variety: A rank of taxonomic groups below the species or subspecies which retains most of the characteristics of the species, but differs in some way such as flower or leaf color or size of mature plant. It is based on minor characteristics and often an exclusive geographic range. A variety is added to the specific binomial name and preceded by 'var.', such as *saxatilis* in the epithet *Juniperus communis* var. *saxatilis*. In some contexts, it is a synonym for cultivar.

Vigor: Relates to the relative robustness of a plant in comparison to other individuals of the same or similar species.

Water repellency: Soil can form a hydrophobic (water resistant) layer during fire that prevents water percolation through the layer and into the soil.

Wildland-urban interface: Areas where wildlands are next to homes and communities; where residential and other developments (recreational, transportation, and so on) have been built into and next to natural habitats. Given the acronym "WUI" in urban forestry jargon, there are many implications to this interface, including issues arising from human-wildlife interaction, trees that now are hazards, fragmentation of plant communities, and removal of vegetation to lower fire risk.

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