Ecological Genetics and the Restoration of Plant Communities: Mix or Match?

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Abstract

We present a conceptual framework for choosing native plant material to be used in restoration projects on the basis of ecological genetics. We evaluate both the likelihood of rapid establishment of plants and the probability of long-term persistence of restored or later successional communities. In addition, we consider the possible harmful effects of restoration projects on nearby ecosystems and their native resident populations. Two attributes of the site to be restored play an important role in determining which genetic source will be most appropriate: (1) degree of disturbance and (2) size of the disturbance. Local plants or plants from environments that “match” the habitat to be restored are best suited to restore sites where degree of disturbance has been low. Hybrids or “mixtures” of genotypes from different sources may provide the best strategy for restoring highly disturbed sites to which local plants are not adapted. Cultivars that have been modified by intentional or inadvertent selection have serious drawbacks. Nevertheless, cultivars may be appropriate when the goal is rapid recovery of small sites that are highly disturbed.

Introduction

There has been an increase in efforts to restore habitats degraded by human activities throughout the world (Berger 1990; Anderson 1995; Hobbs & Norton 1996). Restoration projects vary greatly in size and degree of disturbance to be ameliorated. Managers of national parks and forests attempt to restore vegetation of trails, roads, and campgrounds (Majerus 1997). Oil companies restore drill pads. Prairie restoration projects of all sizes are becoming common (Kline & Howell 1987). Hard rock and strip mines often require intense reclamation (Schaller & Sutton 1978). Logged forests, abandoned agricultural lands, and overgrazed rangelands all require large scale restoration efforts (Millar & Libby 1989; Jackson 1992; Roundy et al. 1995).

In the past, reclamation of degraded land has usually been accomplished with a few species that were often exotic to the disturbed area. But there is growing awareness that restoring ecosystem function and biological diversity often requires the use of native species. Many animals, especially insects, require specific native plants for food (Futuyma 1983). In addition, native plants often provide the specific vegetation structure required for nesting or feeding (Bock et al. 1986; McAdoo et al. 1986; Wilson & Belcher 1989). Furthermore, exotics may compete with native plants (Bock et al. 1986; Lesica & DeLuca 1996) and alter the frequency or intensity of ecosystem processes such as fire (Cox et al. 1990). For these reasons the use of native plants in ecological restoration is becoming increasingly important.

Much of the literature on ecological restoration pertains to the choice of species to be used (Chambers et al. 1984). It is becoming increasingly apparent, however, that intraspecific genetic differentiation in relation to site ecology is also important (Belnap 1995). Many restoration sites, such as mine spoils, pose novel and severe challenges to vegetation, and only specific ecotypes may be able to survive (McNeilly & Bradshaw 1968). On the other hand, plants introduced from distant source populations may not be adapted to the local climatic, edaphic, or biotic environment (Millar & Libby 1989; Knapp & Rice 1994; Linhart 1995).

One goal of restoration is creation of self-supporting communities that will provide ecosystem functions and processes, as well as prevent erosion and provide habitat for diverse native species (Bradshaw 1987). Rapid establishment of plants with a high survival rate is important to prevent erosion and invasion by exotics. In addition, the long-term persistence of restored or later successional communities is also important. Restoration of endangered species populations has received a good deal of attention recently (Bowles & Whelan 1994; Falk et al. 1996), but our concern is with restoration and reclamation of native vegetation rather than reintroduction of rare species.

Relatively little attention has been given to the effects of restoration projects on nearby ecosystems and their native resident populations. Potential threats to local communities and populations from restoration efforts result from the introduction of genes and the loss of locally adapted genotypes. Species are likely to require the genetic variation found throughout their range in order to adapt to future environmental changes. Over
the long term, local genotypes may be crucial to the persistence of populations or the species as a whole (Frankel & Soule 1981).

Opinions differ on the correct strategy for choosing plant materials for restoration (Belnap 1995). Many restorationists use cultivars selected for high performance in restoration situations (Wright 1975; Pater 1995; Shaw & Monsen 1995), while others champion the use of local sources (Knapp & Rice 1994; Linhart 1995). A third strategy uses mixtures of populations or hybrid genotypes (Millar & Libby 1989; Munda & Smith 1995). We cannot recommend a single correct strategy for any specific situation. Rather, we present a conceptual framework for assessing the value of different strategies across a wide array of situations. We approach this problem by first reviewing the underlying genetic principles and then placing these principles in the context of restoration ecology. Finally, we evaluate various strategies for choosing restoration plant materials in light of ecological genetics theory.

**Genetic Principles**

**Local Adaptation**

Numerous studies have demonstrated that plants evolve local ecotypes closely adapted to their immediate environment (Turesson 1922; Clausen & Hiesey 1958; Bradshaw 1972; Turkington & Harper 1979; Linhart & Grant 1996; but see Rapson & Wilson 1988). For example, *Penstemon eatonii* (firecracker penstemon) seed shows apparently adaptive ecotypic differentiation for germination requirements. Seed from high-elevation populations required long chilling periods, while those from low elevations needed only short chill times for germination (Meyer et al. 1995). High-elevation ecotypes may be able to establish an initial population in low-elevation sites, but population growth could be curtailed by failure to recruit a second generation due to inadequate chilling periods. *Atriplex canescens* (fourwing saltbush) populations vary for cold hardiness. Warm desert populations may not survive in cold desert environments following a severe winter (Meyer & Monsen 1992). There is also a great deal of intraspecific variation for disease resistance in plants (Futuyma 1983; Burdon 1987; Augspurger 1988). Pacific slope plantings of interior strains of *Pseudotsuga menziesii* (Douglas fir) have failed due to diseases of little consequence to resident populations (Silen 1978).

While many widespread species demonstrate adaptive genetic variation over their range, others maintain a wide ecological amplitude, apparently by means of one or a few highly adaptable, phenotypically plastic genotypes (Bradshaw 1965). The Eurasian grasses *Bromus tectorum* and *B. rubens* occur in many different environments in western North America, but there is little evidence for genetic differentiation among populations from most of these habitats (Wu & Jain 1978; Rice & Mack 1991). The African grass *Pennisetum setaceum* has adapted to widely different habitats on the island of Hawaii without detectable genetic differentiation (Williams et al. 1995).

**Artificial Propagation**

Strong inadvertent directional selection may occur during cultivation (Knapp & Rice 1994). Production of native plants for restoration involves collection of wild seed, and genetic variation can be lost through inadequate sampling (Brown & Briggs 1991). Assuming that there is genetic variation within cultivated populations, some plants will be more vigorous under cultivation than others. These plants will produce more seed and be over-represented in standard nursery seed collections (Knapp & Rice 1994). It is impossible to predict what these inadvertent selection forces will be (Templeton 1991).

Intentional selection also often occurs during the propagation of native plants for restoration (Voigt et al. 1987; Alderson & Sharp 1994). Several strategies are employed to select for desirable characters such as forage and seed production, seed germinability, and tolerance of salt, heat, and drought. These strategies vary from weak uniparental selection in a single generation to strong recurrent selection (Wright 1975; Vogel & Pedersen 1993).

Selection will increase the frequency of alleles responsible for the desired trait but may also result in the deterioration of other aspects of performance (Hartl & Clark 1989). For example, selection for rapid growth often will also result in shorter life span. The two primary mechanisms of genetic correlation are pleiotropy (one gene having many phenotypic effects) and linkage disequilibrium (selection for one gene will also affect other closely linked genes on the same chromosome). Strong directional selection will also reduce the genetically effective population size and result in increased genetic drift and more rapid loss of genetic variation.

**Genetic Drift**

Genetic drift refers to changes in allele frequency from generation to generation caused by sampling error. That is, the genes transmitted to progeny are an imperfect sample of the allele frequency in the parents. The smaller a population, the greater will be the genetic drift. Genetic drift causes a loss in genetic variation (heterozygosity and allelic diversity) within populations (Nunney & Elam 1994).
Genetic drift is potentially of special concern in restoration because of the so-called “founder effect.” The founding of a new population by a small number of individuals will cause abrupt changes in allele frequency and loss of genetic variation (Barrett & Kohn 1991; Ellstrand & Elam 1993). Such severe population size “bottlenecks” associated with the establishment of a new population are a special case of genetic drift.

Gene Flow

Gene flow in plants—the immigration of nonlocal genes, gametes, or individuals into resident populations—is determined partly by breeding, pollination, and dispersal systems (Levin & Kerster 1974). Higher levels of gene flow occur in insect-pollinated, wind-pollinated, and obligate outcrossing species (Ellstrand & Hoffman 1990) but substantial gene flow (up to 33% hybrids in one generation) can occur even in species that are primarily autogamous (Wilson & Manhart 1993).

Gene flow can reduce the fitness of local genotypes (Slatkin 1985). Neutral, or near-neutral, alleles can be lost from a population by the swamping effect of mass immigration and genetic drift. Swamping becomes more likely as the number of immigrants increases relative to the number of residents. But genes that confer a strong and persistent adaptive advantage are not usually lost from a resident population, even in the face of high levels of gene flow (McNeilly 1968; McNeilly & Bradshaw 1968; Bradshaw 1972; Nagy 1997).

Adaptive genes or multiple gene complexes of resident populations could be lost to swamping if their selective advantage is temporally variable. Drift and high levels of gene flow can act to replace adaptive genotypes during periods when selection is “relaxed.” Many local adaptations may not be apparent during “usual” years but may become extremely important when unusual extreme conditions occur (e.g., drought, floods, or extreme temperatures). For example, many genes that confer disease resistance have a large selective advantage when the target disease is present, but these same alleles are often at a selective disadvantage when the disease is absent (Burdon 1987). The frequency of the resistance gene will cycle in response to the abundance of the pathogen. Loss of a resistance allele from the population could occur if a large immigration of nonresistant genes occurs during that part of the cycle when resistance genes are infrequent and not favored by selection. Cold-hardiness can be swamped out by a fast-growing, cold-vulnerable genotype introduced in large numbers during a period of benign weather. For example, coastal Douglas fir grows faster than inland ecotypes; but coastal ecotypes may survive for many years only to be killed by occasional extreme cold temperatures when planted in interior sites (Silen 1978).

There is also a danger that introduced populations will alter local ecological relationships by transferring adaptive genes to resident populations (Rissler & Melkon 1996). Crop-weed systems are appropriate for modeling the genetic effects of introductions on native populations. Transfer of genes from crops into adjacent, conspecific, or congeneric weed populations regularly occurs (Small 1984; Santoni & Berville 1992). Substantial gene flow (1–89% hybrid progeny) has been reported at distances of up to or greater than 1000 meters in a single generation (Kirkpatrick & Wilson 1988; Langevin et al. 1990; Klinger et al. 1992; Arias & Riesberg 1994). In many cases, gene exchange from crops to weed populations has led to the evolution of more competitive weeds (Pantosos & Baker 1967; Baker 1972; Barrett 1983).

Hybridization

High levels of genetic variation resulting from inter- and intraspecific hybridizations may facilitate adaptation to novel or stressful environments in plants (Anderson & Stebbins 1954; Milligan & Moore 1961; McArthur et al. 1988; but see Whitham 1989; Jain 1994. For example, hybrids between the irises, Iris brevicaulis and I. fulva, occur in habitats unique relative to the parental species (Cruzan & Arnold 1993). Natural hybrids between the sages, Salvia apiana and S. melifera, are rare but are locally common in novel, but disturbed habitats such as abandoned orchards (Anderson & Anderson 1954). Hybrids between two subspecies of Artemisia tridentata (big sagebrush) have higher fitness than either parental ecotype in a novel habitat formed following the last glaciation (Wang et al. 1997).

Populations of multiple ecotypes are likely to show increased long-term stability compared to single-line populations (Marshall & Brown 1973) because natural selection may vary over short distances or periods of time. Different ecotypes of Trifolium hirtum (rose clover) germinate better under different conditions. Thus, colonies started from mixtures of two ecotypes are more likely to persist than monomorphic colonies (Martins & Jain 1979). Stebbins and Daly (1961) studied a hybrid swarm between the sunflowers Helianthus annuus and H. bolanderi in an environmentally heterogeneous site in California. They found that annuus-like hybrids were more abundant in one part of the population, while bolanderi-like hybrids were more common in the other part. It is unlikely that either species alone could have occupied this site as completely as the hybrid population. Hybrid populations will not always outperform single ecotypes on stressful sites, and more research is needed to determine the generality of the hybrid superiority phenomenon in the context of restoration.

In contrast, hybridization between genetically dissimilar individuals may also result in a decline of prog-
eny fitness (i.e., outbreeding depression; Lynch 1991). Two mechanisms can account for outbreeding depression (Templeton 1986; Waser 1993). Under the “genetic” or “intrinsic” mechanism, the parental individuals have different intra-genomic coadaptations that are disrupted in the hybrid progeny. Sterile triploid progeny produced by matings between diploid and tetraploid parents is an extreme example of this. The “ecological” or “extrinsic” mechanism of outbreeding depression results from local adaptation of the parents and the production of progeny less suited to either parental environment (see Local Adaptation section above).

There is evidence for outbreeding depression in plants (Sobrevilla 1988; Barrett & Kohn 1991; Waser 1993); but most examples of outbreeding depression more likely result from the ecological rather than the genetic mechanism (Waser 1993; Wang et al. 1997; but see Whitham 1989). Ecological outbreeding depression can result in the failure of hybrids in parental (i.e., native) habitat, thus helping to prevent swamping of indigenous genotypes following restoration introductions (see Gene Flow section above). But ecological outbreeding depression should not be relevant for disturbed restoration sites because they are different from parental habitats. Genetic outbreeding depression could result in a hybrid zone dominated by individuals with lower fitness than the indigenous population (Whitham 1989).

**Restoration Ecological Genetics**

The genetic constitution of an introduced population is likely to have an important effect on the short- and long-term persistence of the restored and adjacent native populations. Genotypes may be derived from various sources, including local populations, distant populations, or cultivars. Two attributes of the site play an important role in determining which genetic source will be most appropriate: (1) degree of disturbance and (2) size of the disturbance. Both are continuous variables, but for the sake of discussion we treat them as discrete.

**Degree of Disturbance**

Degree of disturbance is the most important environmental variable determining the short- and long-term persistence of populations introduced for restoration. Disturbances can vary from slight degradation to nearly complete devastation (Hobbs & Norton 1996). Local genotypes should be well adapted when severity has been low and the abiotic environment is not very different than before the disturbance. Such sites might include overgrazed range where soil structure remains intact or logged-over forests where post-harvest treatments have not been severe.

On the other hand, severely disturbed sites, such as mine tailings or roadsides where the topsoil has been removed, will pose a novel and often stressful ecological challenge to introduced plants. High levels of genetic variation may be needed for long term persistence in severely disturbed sites (Munda & Smith 1995).

**Size of Disturbance**

The size of the disturbance dictates how much material will be introduced and is important in determining how severely resident populations will be affected. The area to be restored may be small compared to the surrounding native vegetation. Examples include roadcuts, small mines, and oil and gas drill pads. In these situations there is little chance that local adaptive genotypes will be swamped out by introduced genes when the latter are at a great numerical disadvantage. But introduced genes that are adaptive could spread into resident populations.

Larger disturbances, such as strip mines, overgrazed rangeland, or intensively harvested forests, present a different situation because the quantity of introduced genetic material is relatively large compared to that of resident populations immediately surrounding the site. Resident alleles will be at a numerical disadvantage adjacent to the site, and those not presently under strong selection may be lost to drift.

**Restoration Strategies**

A primary goal of restoration is the rapid establishment of long-term viable populations that will restore ecosystem functions and processes, prevent erosion, and protect biological diversity. Restoration should also preserve the ecological and genetic balances present in adjacent native communities. Degree and size of the disturbance are critical factors. Three general strategies are employed to choose genetic makeup for restoration plant material: use (1) genotypes derived from local populations, (2) genotypes selected for high performance in restoration situations, and (3) hybrid genotypes or genotype mixtures with maximum amounts of genetic diversity. We will evaluate each of these alternatives in light of the size and degree of the disturbances being mitigated.

**Local Genotypes**

Local genotypes are best suited to restore sites where the degree of disturbance has been low (Fig. 1). Although close correspondence between environment and genotype argues for the use of local genotypes in restoration (Linhart 1995; Knapp & Rice 1996), soils of seriously disturbed sites bear little resemblance to those
with which natives evolved. Traits found in dissimilar populations may be needed for adaptation to highly novel or stressful conditions. Local genotypes are also desirable when the size of the disturbance is large because they will have no adverse effect on the integrity of local gene pools (Knapp & Rice 1994; Linhart 1995).

Collecting seed from all possible ecological settings within a population will maximize genetic variation without sacrificing local adaptiveness (Knapp & Rice 1994). A single local population may encompass a great deal of adaptive genetic variation correlated with topographic, edaphic, and biotic differences (McGraw 1985; Farris 1987). For example, a species may occur in shallow, stony soils of ridge tops as well as deeper soils of lower slopes. Part of a population may occur in full sun, while the other part may be found in the partial shade of forest margins. Using local genotypes from all possible ecological niches will help ensure the success of this strategy. Millar & Libby (1989), Kitzmiller (1990), Brown & Briggs (1991), Guerrant (1992), and Knapp & Rice (1994) provide guidelines for sampling maximum genetic diversity.

**Hybrids or a Mixture of Genotypes**

Hybrids between populations, or mixtures of genotypes from different populations, may provide the best strategy for highly disturbed sites to which local genotypes are not adapted (Guerrant 1996) (Fig. 1). Mixtures of genotypes from ecologically distinct populations or hybrids of these genotypes will possess high levels of genetic variation. Introduced populations with enhanced variation are more likely to rapidly evolve genotypes adapted to the novel ecological challenges of severely disturbed sites. Using genotypes from a large portion of the species’ range makes complete failure of hybrid populations from environmental incompatibility less likely. Mixture or hybrid populations should also be reasonably well adapted to extreme local conditions if one of the source populations is local. Thus, they should provide both short- and long-term adaptiveness and may be appropriate when the degree of disturbance is high.

Using hybrid mixtures or genotypes will likely introduce novel genes into the adjacent resident population through cross-pollination, although the degree of genetic introgression will depend on the breeding system. Neutral or near-neutral introduced genes will have little chance of spreading widely in the resident population if the size of the restoration is small. On the other hand, large introductions of cultivars could alter the resident neutral gene pool. Furthermore, adaptive genes could be introduced into the resident population regardless of the size of the restoration, although we believe that this danger is less than for cultivars that have been selected for short-term fitness. Using autogamous species or genotypes will lower but not eliminate the risk of genetic transfer. For these reasons hybrid mixtures or genotypes will be most appropriate for restoring smaller disturbances (Fig. 1).

**Selected Genotypes**

Cultivars (selected genotypes) have many serious drawbacks for restoration. Nonetheless, they often perform well in stressful conditions to which local genotypes are not adapted and may be appropriate when the goal is rapid recovery of small sites that are highly disturbed (Fig. 1). Cultivars of native species possessing the ability to rapidly colonize highly disturbed sites are often used in reclamation (Voigt et al. 1987; McArthur 1988; Pater 1995). These ecotypes are chosen or bred for traits such as transplant survival, seed production, seedling emergence, vegetative vigor, drought tolerance, metal tolerance, and competitive ability (Kitchen 1995; Pater 1995). Restoration cultivars often provide the best immediate results, establishing quickly and providing adequate forage or ground cover. In addition, many selected cultivars are readily available from government agencies and private producers.

Unfortunately, cultivars may be poorly adapted for long-term persistence. The distribution of species is often controlled by extreme climatic events such as drought, floods, or periods of hot or cold temperatures. Cultivars are likely to succumb to stochastic environmental extremes when used outside the range of their progenitor population. Furthermore, introduced cultivars may lack resistance to local pests and pathogens. But gene flow from surrounding indigenous genotypes may eventually increase the adaptiveness of introduced populations, especially if they are small compared to the native matrix.

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Figure 1. General relationship to degree and size of disturbance of three possible sources of plants to be used for restoration projects.
Introduced cultivars could transfer adaptive genes to resident populations, possibly resulting in a shift in competitive interactions in the community. This danger is especially great when the introduced cultivars have been selected for fecundity, vegetative vigor, or other traits that promote aggressiveness in the field. Use of self-pollinating species or genotypes will lower the risk of genetic transfer; but moderate levels of gene flow may occur even in primarily selfing plants.

Conclusions

The short- and long-term success of a vegetation restoration project may depend on choosing the appropriate genetic source. The size and degree of disturbance of the area being restored are important variables in determining the source for introduced plant material (Fig. 1). Few situations will be unambiguous, and rigid rules are not practical. Nevertheless, we propose the following general guidelines:

1. Avoid strongly selected cultivars.
2. Initiate new populations with as many genotypes and as much genetic variation as possible (collect seed from many habitats), especially when disturbances have been severe.
3. Use local genotypes when feasible, especially for large sites.
4. Use phenotypically plastic species with wide ecological amplitudes when feasible.
5. Use selfing species or those with low dispersal capabilities to minimize the genetic contamination of resident populations.

We believe that understanding the trade-offs involved is essential in choosing an appropriate strategy. As restoration projects become larger, it becomes more important to use local sources for plant material to lessen the chance of contaminating the resident gene pool. As the degree of disturbance becomes greater, the importance of high levels of genetic variation will increase. Locally derived material may provide adequate variation if it is collected from ecologically varied habitats. Using species with inherently great ecological amplitude resulting from phenotypic plasticity may also prove to be a viable strategy. In severely disturbed sites, however, using hybrid mixtures or genotypes may be desirable to help assure that populations can adapt to the novel or stressful environment. If introduced genotypes are to be used, species with breeding systems that limit gene flow (e.g., selfing) will pose less of a threat to resident populations.

Cultivars selected for aggressive traits, such as vegetative vigor or high fecundity, are undesirable in most situations because they can disrupt the ecological interactions between species and resident gene pools of local communities. They may also fail to provide long-term viability if not derived from local sources.

Many other considerations besides genetics must be taken into account when choosing plant material for restoration. Cost and availability can be critical factors. Planning ahead is important, and increased demand should eventually result in adequate supplies of at least some locally derived material. Some sites may be so severe that only cultivars selected for stress tolerance will be able to establish vegetation cover within a reasonable time frame. While it is essential to quickly establish vegetation that will provide cover and prevent erosion, it is equally important to protect the genetic structure and ecological interactions present in the native mosaic of locally adapted populations.

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